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COMPETITION AND COEXISTENCE OF CLONAL PLANTS IN RELATION TO PRODUCTIVITY

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

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1. Sammul, M., Kull, K., Oksanen, L., Veromann, P. 2000. Competition intensity and importance: results from field experiments with *Anthoxanthum odoratum*. Oecologia 125:18–25.

2. Sammul, M., Oksanen, L., Mägi, M. Competition intensity, productivity and species richness: a field experiment in two distant regions. Manuscript.

3. Tamm, A., Kull, K., Sammul, M. 2002. Classifying clonal growth forms based on vegetative mobility and ramet longevity: a whole community analysis. Evolutionary Ecology 15:383–401.

4. Sammul, M., Kull, K., Tamm, A. 2003. Clonal growth in species-rich grassland: the results of a 20-year fertilization experiment. Folia Geobotanica 38:1–20.

5. Sammul, M., Kull, K., Niitla, T., Möls, T. A comparison of plant communities on the basis of their clonal growth patterns. Manuscript.

INTRODUCTION

You have your theories, and I got one too
It's such a waste

Dean Wareham

Productivity gradient is one of the most utilized environmental gradients in ecological studies. It has been shown to correlate with several phenomena, such as species and growth form composition of the community (Whittaker 1975, Grime 1979, Tilman 1988) and trophic interactions (Oksanen et al. 1981, Reader 1992). Most influential for plant ecology has been the phenomena of changing species density with changing productivity (Grime 1979, Grytnes 2000). It has been repeatedly shown that there exists a unimodal relationship between plant species density and productivity of the system (Grime 1973, Al-Mufti et al. 1977, Zobel & Liira 1997). The maximum species richness is found in moderately barren habitats. With increasing productivity species density declines. Several fertilization experiments have confirmed this result by showing that fertilization significantly reduces species richness of plant communities (Grime 1979, Huston 1979, 1994, Austin & Austin 1980, Willems et al. 1993, Mountford et al. 1996, Hansson & Fogelfors 1998).

The main cause of such decline in diversity has commonly been argued to be the increase in competition intensity. For a couple of decades, plant ecologists have intensely debated whether there is a relationship between productivity of plant communities and intensity of competition. However, despite a number of experiments in which the relationships between competition intensity and main community parameters were analysed (Putwain & Harper 1970, Silander & Antonovics 1982, Berendse 1983, Keddy 1989, Aerts et al. 1990, Di Tomasso & Aarssen 1991, Wilson & Tilman 1991a,b,1993, Gerry & Wilson 1995, Kadmon 1995, Herben et al. 1997a, McLellan et al. 1997), there is yet no general agreement on how competition changes along the principal natural gradients. Moreover, despite an intense discussion about the effect of competition on species richness of the community the relationship between competition intensity and species richness has been directly studied in only a few studies (Gurevitch & Unnasch 1989, Lepš 1999, Wardle et al. 1999, Smith et al. 1999, see also reviews by Aarssen & Epp 1990, Goldberg & Barton 1992).

One of the common features of the communities with very high species density is that they consist mostly of clonal plants (Kull & Zobel 1991, Kukk & Kull 1997, Cantero et al. 1999, Klimeš et al. 2001). These communities are also semi-natural in a sense that they need mowing or grazing with low intensity for their persistence while they are otherwise unmanipulated, i.e. no ploughing or fertilization or seed

sowing has been used to manipulate their species composition. Mowing results in a disproportional removal of tall plants, which are commonly considered as competitively superior (e.g. Grime 1973, 1977). Thus, continuous low-intensity management by mowing or grazing has a disproportionately large effect on competitive dominants, and by reducing the asymmetry in size distribution of plants it reduces the intensity of competition for light (Lepš 1999). The effect of reducing the asymmetry of interactions is further amplified by equalling also other aspects of dynamics of plant populations, such as mortality, sexual reproduction and vegetative reproduction, which are commonly ramet size-dependent (Barkham 1980, Pitelka et al. 1985, Weiner 1988) and are part of competition for space. Therefore, the competitive exclusion, if present, should be a slow process in extensively managed semi-natural communities. And even more so, if the community is dominated by clonal plants, since it has been shown that competition in clonal plants is much more symmetrical than in non-clonal plants (de Kroon et al. 1992, Hara 1994, see also Suzuki & Hutchings 1997), owing partly to the physiological integration between ramets within the clonal fragment (Caraco & Kelly 1991, Stuefer et al. 1994, Gough et al. 2002 and references therein).

The population dynamics of clonal plants differs from that of non-clonal plants in many aspects. Persistence of organs with capability for resource storage changes the allocation of assimilates and amount of available resources to seed production (Ogden 1974, Carlsson 1990). Clonal offspring has greater survival compared to survival of seedlings (Callaghan 1984, Muir 1995, Cain & Damman 1997). Several species of clonal plants can selectively place the offspring to more favourable patches (de Kroon & Hutchings 1995) or to the safe distance from mother ramet to avoid self-thinning or other density-dependent negative effects (Hutchings 1979). Moreover, by selection of patches for offspring clonal plants choose the identity of neighbours and correspondingly change the rate of inter- to intra-specific (and/or intraclonal) interactions (Lovett Doust 1981, Maddox et al. 1989). Clonal growth reduces the risk of mortality for the genet (Cook 1979) and for the physiologically integrated ramets within clonal fragment (Pitelka et al. 1985). The capability of vegetative reproduction and long life-span of ramets enable the genet to withstand periods of non-successful seed production or seedling establishment (Chesson 1985, Chesson & Huntley 1988, Carlsson 1990). Differences in the use of space and vegetative mobility change the rate of local vs. long-range dispersal and expansion into new habitats (Lovett Doust 1981, Angevine & Handel 1986), affect the likelihood of outbreeding (Cook 1983) and consequent pattern of genetic recombination. Altogether the population dynamics of clonal plants is primarily different from non-clonal plants in the way the plants occupy open patches in the community and in that clonal plants may keep an occupied patch for many years.

The spatial distribution of individual ramets determines largely the fate of interspecific interactions. Therefore, to have a complete overview of interactions in communities where clonal plants dominate, it is important to understand the role of vegetative mobility and clonal propagation there. The notion of non-uniform

(clumped) distribution of individuals and populations in space (van der Maarel 1988, Tilman & Kareiva 1997) and observations of permanent plots with high spatial resolution (van der Maarel & Sykes 1993, Herben et al. 1994) have led to the view that there exists considerable spatio-temporal turnover of ramets (van der Maarel & Sykes 1993, Sykes et al. 1994, Herben et al. 1997b). This in turn is largely dependent on the clonal growth form of the constituent species (Law et al. 1994, Herben et al. 1995).

There are several classifications of clonal growth forms which aim to describe the whole variety of clonal growth types (Klimeš et al. 1997), have concentrated on the spatial pattern of distribution of shoots (guerilla- and phalanx-type growth; Lovett Doust 1981, Harper 1985), or are based on the characteristics of persistence of integration between ramets (Jónsdóttir & Watson 1997) or on the characteristics of the regeneration (Eriksson, 1997) of clonal plants. Rarely, however, the specific role of individual traits of clonal propagation or clonal growth forms in community dynamics and species coexistence has been analysed (but see Klimeš et al. 1997). It is has been shown in wetlands of China that number of plant species in the community increases with increasing abundance of phalanx species and decreasing abundance of guerilla species (Song & Dong 2002). In risky environments the compensation for high mortality rates by increased establishment from seeds is considered of higher value for survival than clonal growth (Barkham & Hance 1982). In resource-poor environments extensive integration between ramets should be advantageous (Jónsdóttir & Watson 1997). However, there is still not much information on how certain clonal growth traits are related to environmental conditions or species interactions.

Because of their sedentary nature, plants are affected primarily by local environmental conditions and by biotic interactions among nearest neighbours. Interactions take place between ramets (or clonal fragments) that are located close enough to each other so that their zones of influence overlap (Gates & Westcott 1978). Thus, spatially local conditions strongly affect the dynamics of plant populations (Cain et al. 1995). Clonal plants have the ability to form monospecific stands of various size and stability (Hutchings 1979) and this way change the species composition of their nearest neighbourhood and affect local conditions on a micro-scale. It has been shown that these stands, which are usually a product of a growth of a single genet, may resist competition from other species (Ogden 1974, Grime 1977, Barkham & Hance 1982) and enhance persistence of a clone (Pitelka et al 1985). Extensive root systems and ability to expand laterally are advantageous characteristics and may enhance the competitive success (de Kroon & Bobbink 1997). To competitively exclude an individual, the zones of influence of competitors must largely overlap for sufficient amount of time. Clonal plants which grow in tussocks may considerably diminish this overlap and shading by other plants by expanding their tussocks horizontally. There may even be a plastic response to neighbour presence as vegetative mobility of species may decrease with increasing neighbour density (Cheplick 1997, Humphrey & Pyke 2001).

On the other hand, it has been shown that interspecific difference in mobility promotes coexistence in modelling studies (Bell 1984, Caswell & Cohen 1991) as well as in experimental communities (Schmid & Harper 1985, Klimeš 1999). Clonal mobility may be an especially effective way to alleviate or delay competitive exclusion (Bell 1984, Herben et al. 1994) as mobile plants may escape competition by moving to another unoccupied spot. Moreover, some clonal plant species even have the ability to selectively place their offspring in more favourable patches (see reviews by Hutchings & de Kroon 1994, de Kroon & Hutchings 1995) considering both distribution of nutrients and presence and identity of neighbours. It is thus still unclear which clonal growth type is most effective in competitive situations and whether different environmental conditions affect success of certain clonal growth form. Obviously, there is not enough information on influence of species interactions on clonal plants and it is not known to what extent changes in species composition due to competition are influenced by the traits of clonal propagation of competitors.

The distinction has been made between the effect of competition on the single ramet (or clonal fragment) and on the whole population or the community structure (Welden & Slauson 1986, Goldberg 1994, Goldberg & Novoplansky 1997). Most of the studies have dealt with the former and measured the impact of competition or other interactions to the growth of the individual ramets and often also during short period. To approach the effect of species interactions to the structure and composition of the whole community one should concentrate on the parameters that determine dynamics of populations, i.e. mostly on changes in parameters of reproduction of plants or on population dynamics of competing species. Mechanistic approach to the vegetation dynamics requires that simple biologically meaningful and easily measurable characteristics of clonal propagation would be used. I have used the following characteristics of individual ramets, which are important with regard to population and community dynamics (see also Kull 1995, Herben 1995):

A) Ability to spread and occupy new patches. 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).

B) Plant unit area (PUA, van der Maarel 1988, Zobel & Liira 1997) or the surviving zone (Gates & Westcott 1978) or minimal patch size. It is the size of the area occupied by one ramet. PUA is evidently related to shoot size and growth form of the species.

C) Length of the period during which a genet holds one patch. There are two ways for a genet to persist in a patch. First, if the ramet is perennial and not moving, it stays within one patch for as long as it lives, i.e. as long as the life span of a (immobile) ramet. Second, a ramet that inhabits a particular patch (mother ramet) may produce new (daughter) ramets which are located in the same patch and thus persist there after the death of the mother ramet. This

type of patch-holding can be estimated via measurement of the amount of "short" rhizome branches per ramet.

These traits determine population dynamics of populations of clonal plants, and when estimated for the whole community can shed light to interactions in community and formation of structure of herb-layer of plant communities. Still, the studies where clonal growth of all species in the certain community were estimated and compared to some other community (e.g., Pokarzhevskaya 1995) or compared with the same community after some kind of perturbation are very few.

This thesis sums up studies that are performed to estimate the role of vegetative propagation in shaping the pattern of species distribution along productivity gradient. I will concentrate on changes in intensity of interactions and in abundance of species with different traits of clonal growth in communities with different productivity, since I presume that these changes affect species richness.

I start with a test of the presence of relationship between competition intensity and community productivity in clonal plants (I, II). Since it is often only presumed that increase in intensity of competition reduces species richness I analyse whether there is such a relationship (II). The species that gain in abundance and become dominants with increasing productivity may have certain common traits. To test for the presence of common traits of vegetative propagation in such species, the classification of clonal growth forms is developed (III) and the distribution of species with different characters of clonal growth on natural (III, V) and experimental (IV) productivity gradients examined. As clonal plants dominate in species rich systems, I investigate the relationships between traits of vegetative propagation and species richness (III, IV. V). I also evaluate the effect of productivity to the overall ramets' mobility pattern and ramet turnover in the community and discuss the consequences of ramet mobility and turnover to the species richness (IV, V).

METHODS

Study areas

Laelatu wooded meadow

Laelatu wooded meadow is located on the western coast of Estonia (58° 35' 15" N, 23° 33' 00" E) on the West Estonian Lowland. 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. Mean temperature for July is 17°C and for January –5°C. Annual mean temperature is 6.3°C in the air and 7.1°C on the ground. Mean annual precipitation is 500–600 mm, the most rainy seasons are late summer and autumn.

The vegetation of 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 - Filipendula hexapetala* association (Krall & Pork 1970). The tree layer (crown projections) covers on average 30–50% of the ground surface and consists of *Quercus robur* L., *Betula* spp., *Fraxinus excelsior* L., *Populus tremula* L., etc. (Kukk & Kull 1997; nomenclature follows Kukk 1999). The flora of vascular plants in 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).

Joatkanjáv'ri field station

In northern Norway, the experiment was conducted near Joatkanjávri, Alta, Finnmark (69°46'N, 23°58'E); altitudes 380–600 m above sea level. The lower parts of the area belong to the hemiarctic zone, where tundra prevails but woodland patches occur in topographically favourable sites. The area includes tundra meadows, lichen heaths, willow thickets and birch forests, although most of the area is devoid of trees. Above the 450 m, the landscape is arctic-alpine: trees are absent

and the vegetation is dominated by small willow shrubs and ericoid plants. The area has an arid climate, annual precipitation being 350 mm, and the mean temperature for July 10°C and for January –10°C.

Rocks are acidic, but nutrient-rich, non-calcareous shifts abound along the thrust line of the Scandinavian mountain chain. Primary productivity is influenced by several factors (altitude, exposition, edaphic moisture, and bedrock). Highest productivities are found on the lower parts of the thrust line, where all local factors are maximally favourable. Lowest productivities are found on summits and in late snow-beds (Oksanen & Virtanen 1995).

Removal experiments (I, II)

In both experiments, the removal of neighbouring vegetation around naturally established target plants was applied to estimate the intensity of competition. In manipulated plots, the above-ground parts of all species, except for *Anthoxanthum odoratum* (I) or *Solidago virgaurea* (II), were removed several (3–5) times in a season.

The response of target plants to removal of neighbours was measured by counting the number of shoots on the plot, and measuring the length of all shoots (I) or counting the number of leaves (II). At the end of the experiments the biomass of all plants was collected from all plots and the dry weight measured. For *Anthoxanthum* (I) only its above-ground biomass was collected, for *Solidago* (II) both above- and belowground biomass was collected.

Fertilization experiment (IV)

In 1961, a fertilization experiment was set up by K. Pork in a uniform, open, relatively dry, old, and the most regularly mown 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 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. 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. All plant parts (excl. litter and woody parts) in samples were thereafter sorted according to species, dried and weighed. The relative proportion in weight was calculated for each species and used as an input value for data processing.

Vegetation censuses along natural gradients (III, V)

A total of 104 vegetation analyses were carried out using 1 m^2 plots. These relevés were located in 13 different sites ranging from deciduous forests and overgrown wooded meadows to wooded meadows and seashore meadows totally devoid of trees. The communities were chosen to provide the full gradient of direct sunlight available to ground layer.

Mostly 8 plots per community were analysed (Table 1 in III). In each plot all species were recorded and their cover (%) estimated. In addition, the number of shoots was counted in two 0.1×0.25 m^2 subplots within each plot. The subplots were located in opposite corners of the 1 m^2 plot and 15 cm inside from both nearest sides of the plot. All shoots in the subplot were cut close to the ground layer, collected, dried at the 80 °C for 48 hours and weighed with an accuracy of 0.1 g to estimate the above-ground living phytomass of the community. Light availability to the ground layer was measured above the herb layer by using a fish-eye photographic technique. Light availabilities were expressed as the light penetration coefficient (Anderson 1964). In each community also the frequency of mowing was recorded using information from managers of the area.

Measurement of plant characteristics (III, IV, V)

Clonal fragments (polycormons) of 120 species (these which were most abundant in the plots of the fertilization experiment) were excavated between 1988–1997 (mostly 1995–1996) for measurement of clonal growth parameters. The plants were mostly excavated from close proximity to experimental plots, from 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. Using scars from dead shoots on rhizomes as well as size and morphology of internodes and nodes on rhizomes, for all ramets their age was estimated, annual increase of their rhizome parts was measured, and the number of rhizome branches per ramet was counted. Later also the number of short rhizome branches (< 10 mm) per ramet

was calculated. 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.

Due to very asymmetric distribution of all measured clonal growth parameters within species 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 (Table 2 in III, Appendix in IV). These parameters of clonal propagation together with respective maximum values (used in classification of clonal growth forms, III) or 0.9 percentiles (which are less sensitive to random factors of sampling than value of maximum, IV V) were used to calculate community-wide clonal growth parameters.

Data processing

To measure competition intensity at first (I) the index of relative competition intensity (*RCI*) was calculated as:

$$RCI = (P_m - P_c) / P_m \quad (1),$$

where P_m is the measure of plant performance on manipulated (neighbours removed) plots at the end of experiment and P_c is the measure of plant performance on control plots at the end of experiment. The number of shoots, mean shoot weight and total biomass of *Anthoxanthum odoratum* were used as measures of plant performance.

Further on (II), *RCI* was corrected for two built-in biases by using the larger of the treatment and control biomass as the denominator and by performing arc sin transformation. The corrected index of relative competition intensity (*CRCI*) was thus calculated as:

$$CRCI = \arcsin ((P_m - P_c) / (\max P_m, P_c)) \quad (2).$$

In this case the total biomass of genets of *Solidago virgaurea* was used as a measure of plant performance.

The community-level estimate of each clonal growth parameter was calculated as weighed average with relative abundance of species as a weight (III, IV, V):

$$M_p = \sum a_i p_i \quad (3).$$

Here M_p is the weighed average of the p^{th} clonal growth parameter, a_i is the estimate of abundance for species i in the plot and p_i is the value of a clonal growth

parameter for species *i*. In fertilization experiment (IV) the biomass share (from 0 to 1) of each species in every plot was used as the estimate of abundance, in case of natural gradients (III, V), cover of each species in every relevé was used as the estimate of species abundance.

To classify clonal growth forms we used cluster analysis (III). This analysis was based on a matrix of presence or absence values of clonal growth characteristics. The Unweighted Pair Group Method using arithmetic mean (UPGMA) was applied and the squared Euclidean distance was used as the sample dissimilarity measure. Classification was performed by using SAS statistical package (version 6.12, SAS Institute Inc., Cary). Differences in Least Square Means of the relative abundance of clonal growth form groups in different community types were estimated with the GLM procedure using the ESTIMATE statement for comparisons.

To estimate impact of biomass, light availability, mowing regime and site on species density, ramet density and community clonal growth parameters the GLM MIXED procedure was applied (V) using statistical package SAS. Studied communities were treated as levels of random factor. Type 3 test of fixed effects was used with the iterative Restricted Maximum Likelihood (REML) procedure to estimate the effect of variance components. To test for dependencies of variables on biomass, light availability and different mowing regimes within one type of the community as well as for differences in average values of variables between the three types of community statement ESTIMATE was used. General relationships between these factors and variables were estimated using a squared correlation matrix with Pearson *r*. The intrinsic relationships between community clonal growth parameters, ramet density and species density were estimated with Pearson partial correlation coefficient. To do that light, biomass, their squared effects and combined effect were kept constant as partial variables. Partial correlations were calculated for the whole data set and for each of the three community types separately. To correct for mass effect, the Bonferroni type correction with Dunn-Šidák method (Sokal & Rohlf 1995) was used where appropriate.

In other cases standard statistics (ANOVA, MANCOVA, Tukey HSD test, correlation analysis, regression analysis etc.) were applied to compare effects of different experimental treatments or relationships between different variables.

RESULTS

Competition intensity, productivity, and species richness (I, II, IV)

Competition intensity was shown to be positively correlated with primary productivity both when *Anthoxanthum* or *Solidago* were used as target species (Fig. 2 in I, Table 4 in II, Fig. 2 in II). In both cases the weight response was detectable only as the response of the whole plot (aboveground biomass per sample plot in *Anthoxanthum* and total genet weight in *Solidago*). In *Anthoxathum* most sensitive to removal of neighbours was the number of shoots on the plot (Fig. 2 in I). In *Solidago* the number of ramets covaried with the genet biomass and was one of the reasons behind the biomass increase in response to neighbour removal. Almost all new ramets in the *Anthoxanthum* experiment and all new ramets in *Solidago* experiment were the result of vegetative reproduction.

The relationship between competition intensity and species richness was estimated in paper II. There was a negative correlation between species density and competition intensity in Estonia (Fig. 3, Table 5 in II). No significant relationship was found between species richness and CRCI in Norway or in pooled (Estonian and Norwegian) data.

Experimental increase of productivity (IV) markedly reduced the number of species in fertilized plots (Table 1 in IV). The more fertilizers were applied the less species were found in the plots after 20 years of experiment, although the differences between individual plots were remarkable. The proportion of species that invaded the plots during the experiment did not differ in different fertilization treatments. The proportion of species that persisted in the plots throughout the experiment decreased with increasing amount of fertilizers applied and the proportion of species that disappeared from the plots in the course of the experiment increased with increasing fertilization (Fig. 1 in IV).

Classification and distribution of clonal growth forms (III)

Our cluster analysis (Fig. 1 in III) revealed three major groups of species according to ramet longevity: (a) species with annual ramets, (p) species with perennial ramets, and (b) species with mostly biennial ramets. Within each of these three groups, species were further subdivided according to their vegetative mobility. These sub-groups contained species with (1) low, (2) medium, (3) and high mobility (Table 3 in III). To thus obtained nine groups two groups of species without the

ability for clonal growth were added: annual species without clonal reproduction (g1) and perennial species without clonal reproduction (g2).

The relative abundance of species with annual ramets (clonal growth types a1, a2, a3) was higher in open meadows (28%) than in restored and overgrown wooded meadows (16% and 15%, respectively; Table 4, Fig. 2 in III).

The relative abundance of species with low vegetative mobility (clonal growth types a1, b1, p1) was higher in open (39%) and in restored wooded meadows (36%) than in overgrown wooded meadows (20%). In contrast, the relative abundance of species with high vegetative mobility of ramets (clonal growth types a3, b3, p3) was higher in restored and in overgrown wooded meadows (39% and 34%, respectively) compared to open meadows (16%). Species with a medium vegetative mobility (clonal growth types a2, b2, p2) had a higher relative abundance in open meadows (31%) than in overgrown (17%) or restored wooded meadows (14%).

Influence of productivity on clonal growth of the community (IV, V)

Experimental increase of productivity of the system (IV) revealed the significance of the composition of fertilizers on the results. Addition of potassium and phosphorus (PK-treatment) significantly increased the abundance of more mobile species (legumes) while with increasing addition of nitrogen the species with lower mobility (tussock grasses) gained in abundance (Fig. 2 A in IV). The abundance of species with higher ability of rhizome branching changed in a somewhat similar way, increasing in treatments with potassium and phosphorus fertilization. When nitrogen was added, species with higher branching intensity gained in abundance during the experiment, although this gain was smaller than in the PK-treatment (Fig. 2 B in IV).

Fertilization reduced the abundance of species with long ramet life span. By the end of the experiment the biomass share of such species decreased in the plots with bigger amount of fertilizers used (Fig. 2 C in IV). There was also a non-significant decrease in the abundance of species placing their offspring close to parent ramets with fertilization (Fig. 2 D in IV). Both latter changes mark the decrease in the time one genet can occupy a certain patch with increasing fertilization pressure.

The analysis of changes along natural productivity gradient (V) confirmed that ramet life span decreases with increasing productivity (Fig. 1 A in V). It was also found that vegetative mobility in the community is negatively correlated and branching intensity is positively correlated with productivity of the community (Table 3 in V). Still, when more sophisticated mixed model was used to analyse relationships between environmental factors and characteristics of vegetation (incl. average clonal growth in the community), most of the correlations were not

supported. This was due to covariation of different factors and their very high within-community variation.

Relationships between clonal growth and species richness (IV, V)

There were only a few direct relationships found between species richness and community-wide clonal growth parameters. Average ramet life span in the community was positively correlated with number of species both in fertilization experiment (Fig. 3 in IV) and on natural conditions in open meadow sites (Fig. 3 A in V). However, it was found that there are considerable differences between different types of communities regarding this relationship. There was statistically significant ($p<0.001$) difference in respective partial correlation coefficient between open meadows and wooded meadows, the latter showing negative correlation between species density and average ramet life span in the community.

It was also found that there is a negative partial correlation between community vegetative mobility (rhizome increment) and species density in wooded meadow sites ($r=-0.54$; $p=0.0036$), and positive partial correlation between branching intensity and ramet density in forests ($r=0.61$; $p=0.0002$). When all three types of communities were analysed together, it was found that all three community clonal growth parameters are partially correlated with each other and coefficient of variation of rhizome increments of coexisting species is partially negatively correlated with branching intensity. There also was a positive partial correlation between species density and ramet density, and between ramet density and branching intensity (Table 6 in V).

DISCUSSION

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, dynamics of these communities depends largely on the success of clonal propagation of different species. Community-level regularities in the distribution of different clonal life-history types provide new information about mechanisms underlaying control of population dynamics of clonal plants, since the parameters of clonal propagation refer directly to the causal processes responsible for the formation of community structure.

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 are the values of these parameters for a species, the bigger is the ability of the species to gain new space and propagate. Ramet life span estimates 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 population dynamics in perennial herbs (see also Herben et al. 1993, Sykes et al. 1994, Herben & Hara 1997, van Groenendael 2000).

It is well known that there are species that have 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, most studied species seem to lack the capability for plastic change of the length of the rhizome (see de Kroon & Hutchings 1995) and only a few studies have reported degrees of plasticity of runners which make plants capable for responding to environmental patchiness in natural conditions (cf. Stuefer 1996). The traits of clonal growth have a species-specific quantitative range of variation as do several other quantitative traits of species (e.g., Grime & Hunt 1975, Ellenberg 1974, Grime et al. 1988). Therefore it is possible to estimate the variation of average clonal growth in different communities by calculation of weighed average of the clonal growth parameter with some estimate of the abundance of each constituent species in the community as a weight. Moreover, communities can even be discriminated using clonal growth parameters thus obtained.

This study shows that there are differences in distribution and abundance of different clonal growth forms between different communities. Even the relationships between some environmental factors (e.g. productivity) and abundance of species with certain clonal growth characteristics may change from community to community. It is expected that forest floor community is way different from herb-layer of wooded meadows and open meadows. Light limitation of growth of forest floor species and considerably lower ramet density show that stress prevails over competitive interactions there. I found rather large variation in average clonal growth parameters in forest floor communities which is partly caused

by differences in growth forms of tree seedlings and herbaceous plants. It is interesting that herbaceous species capable of dominating in forest floor have such a long ramet life span. I hypothesized that partly this may be related to the longevity of light gaps under tree layer. Together with small density of ramets and low intensity of competition there should be not much pressure on the survival of genets in forest floor due to interactions with other herbaceous plants. Much more important is the search for gaps and establishment in suitable patch. In forest floor communities prevailing herbaceous plants have an ability to move long distances not only by seeds but also vegetatively. The ability to move long distance is a necessary precondition for finding a suitable place considering the scale at which the heterogeneity of light occurs in forested areas (see also Stuefer 1996). The growth form, in which ramets may move long distance vegetatively during their first year of life and then inhabit chosen spot for a long time seems to suit well into the forest environment, where light gaps are spatially separated, but relatively long-lasting. Thus, species that can at least to some degree show a foraging tactics of growth are favoured in forests (see also Macdonald & Lieffers 1993).

On open meadows, however, both average ramet life span and vegetative mobility decrease (see also van der Maarel 1996). Considering also slightly higher branching intensity in open meadows compared to other communities one can conclude that phalanx species prevail in these communities. Indeed, species that grow in tussocks (e.g., *Molinia caerulea*) or very densely (e.g., *Sesleria caerulea*) were dominating in most of the open meadows I studied in paper V The dominance of tussock species is dependent on the fact that these communities are not regularly mown. In such conditions competition between species prevails and species density drops. Together with decreasing species density also average ramet life span in the community decreases, which is partly related to the fact that tussock species often have annual ramets, but may also be a direct result of increase in intensity of competitive interactions between neighbouring ramets. The more intense the competition is, the faster inferior competitor gets suppressed and excluded, and even more so, if the ramets are immobile as is commonly the case in species with perennial ramets.

It was confirmed with two different target species in two very distant regions of northern Europe that competition intensity is increasing with increasing productivity of the community. However, the effect of competitive interactions is revealed mostly on the population level. With respect to community dynamics the size of individual ramets is only important if it is related to reproductive success of this ramet and, thus, to population dynamics. The study with *Anthoxanthum odoratum* (I) showed, however, that competition also may act directly on the reproductive behaviour of species (see also Humphrey & Pyke 1998). Clonal plants possess reserves of resources, amount of which is determined by environmental conditions (incl. interactions with neighbours) and by morphology of storage organs of the species (Suzuki & Stuefer 1999). Even a small amount of stored nutrients may

suffice for survival of a genet for, e.g., one season if competition is not very severe. After that mobile species may try to establish in new patch or if species is not mobile there is a hope that competitive pressure is revealed in the next season, e.g. since competitively superior neighbour was with annual ramets or somehow damaged. Moreover, physiological integration between interconnected ramets (Pitelka & Ashmun 1985, Stuefer et al. 1994) may also reduce the negative effect of neighbours (Hartnett & Bazzaz 1985, Williams & Briske, but see Schmid & Bazzaz 1987, Pennings & Callaway 2000). In any case, the survival of a genet can be thus enhanced. However, the reduction of resource acquisition must have some effect. Clonal reproduction is effective only when there is a surplus of assimilates in ramet that reproduces (Caraco & Kelly 1991, Suzuki & Stuefer 1999, Welham et al. 2002). The results of my competition experiments show that when assimilation is reduced by the presence of neighbours clonal plants reduce their vegetative reproduction. It could be that studies which have not found competition intensity increasing with increasing productivity (e.g. Wilson & Tilman 1991a, Peltzer et al. 1998) or have it found decreasing (e.g. Davis et al. 1998, Goldberg et al. 1999) have not taken in account the possibility that in clonal plants the effect of competition is through reproductive behaviour (but see Reader & Best 1989). Moreover, many studies with such results use only experiments lasting no more than one growing season (e.g. meta-analysis by Goldberg et al. 1999), while it takes at least two seasons to detect success of reproduction. Furthermore, clonal plants usually have some perennial organs which may constitute large part of the biomass. Thus, even the response of growth takes many seasons to become distinguishable.

The decrease of population density and/or speed of vegetative reproduction due to competition increases with the increasing size of neighbouring plants. This corroborates to the idea that competition intensity should increase with increasing productivity when survival or community structure is assessed but not when growth of individuals is measured (Goldberg & Novoplansky 1997). On the low productivity end of the gradient tall species may lose their advantage over small species, since they can not grow big enough to outcompete smaller species. The same effect can be seen in case of mowing or grazing which reduce disproportionately more biomass of big plants compared to small ones. Empirical data from species-rich communities shows that these are characterised by small vegetation, low productivity, and extensive management (Grime 1973, 1979, Kull & Zobel 1991). All three seem to relate to low competition intensity, at least to low competition for light. The dynamics of species richness in many fertilization experiments including the one at Laelatu are another indirect evidence that when productivity of the system is increased competition gets more intense (see also Rajaniemi 2003). In studies reporting decreasing species richness with increasing productivity, increasing competition for a single resource, such as light or space, is often proposed as an explanation for the pattern (e.g. Grace & Pugesek 1997. Grytnes 2000). It has been argued that high productivity increases the likelihood of

a strong limitation by a single resource (Grime 1973, Connell 1978, Tilman 1988, Huston & DeAngelis 1994). The evidence analysed so far, and in this study, suggests that local species richness declines along the gradients of increasing productivity if and only if the intensity of competition increases (Goldberg & Estabrook 1998, Peltzer et al.1998, Rajaniemi 2003). Moreover, the relationship between competition intensity and species diversity could be strong in systems with a large species pool, such as the Estonian grasslands on limestone bedrock. Large species pool is a necessary precondition for having many species capable for growing in any community (Wisheu & Keddy 1996, Zobel 1997), thus also in communities with low productivity and low competition intensity.

The studies of species pools have recently been dominating over the studies of effects of local interactions on species richness (e.g. Hodgson 1987, Ricklefs 1987, Taylor et al. 1990, Zobel 1992, Pärtel & Zobel 1995, Pärtel et al. 1996). Yet, the operational definition of species pool states that only species that are able to migrate to the community relatively rapidly are included into the pool (Pärtel et al. 1996). This means that species should grow in a nearby community for being included in the list of local flora. Thus, the species must have locally survived in the process of competitive exclusion.

While species pool indeed sets the upper limit for the number of coexisting species (Zobel 1997, Herben 2000, Gaston 2000), local processes determine the number of species actually coexisting in a given community. The results of this study show that competition causes the decrease in local species richness in calcareous communities. This is concordant with the very rapid decrease in species richness in abandoned wooded meadows (Kukk & Kull 1997), on those alvars, which are no longer grazed (Pettersson 1958), and on several other meadow communities where mowing is stopped (Willems 1983). Moreover, local processes such as cessation of grazing may influence species pool as exemplified by the currently threatened status of several alvar plants. Even the species pool of lime-rich mountain and tundra areas can be crucially dependent on grazing which prevents competitive exclusion of smaller species. It is easier to understand the origin of both large-scale patterns as well as local patterns, if we assume that local processes are crucial for their development and that the role of long time spans and climatic stability (Zobel 1992, Tilman 1997, Grace 1999, Smith & Knapp 2001) is that under these conditions, evolution driven by local processes can successively enrich the flora. If, however, undisturbed competition for a single resource prevails, competitive exclusion will rule, and no amount of time and stability will lead to increased species richness, neither locally nor regionally.

There is not much information available yet on how clonal propagation or vegetative mobility may influence species interactions and species composition of the community. Almost always the species which take advantage of undisturbed competition and changing environmental conditions are clonal (e.g. Bobbink &

Willems 1987, Soukupová 1992 and references therein). Yet, the most species-rich communities also consist mainly of clonal species (Kull & Zobel 1991, Kukk & Kull 1997. Cantero et al. 1999, Klimeš et al. 2001). If the species richness were a community characteristic, determined mainly by the type of the community and corresponding species pool (see also Zobel et al. 1994), then in species-rich habitats no species could have high maximum population density and equally small reduction of potential maximal population density were expected for all species. If species richness is the result of ecological processes that reduce dominance, then population density of potential dominants should be reduced more than that of potential subordinant species.

In case of undisturbed competition the plants that start to dominate and reduce species density of the community, commonly belong to certain growth forms. In case of herbaceous plants they often are growing in tussocks which are highly resistant to invasion of inhabited patch by other species (e.g. *Molina caerulea*), or they may have an ability of quick clonal spread and uniform filling of the area (e.g., *Brachypodium pinnatum*, see also Cheplick 1997, de Kroon & Bobbink 1997, Suzuki & Hutchings 1997. Herben & Hara 1997, Humphrey & Pyke 1998). It has been shown that mobility of a species decreases when competition intensity increases (Cheplick 1997. Humphrey & Pyke 2001) or that taxa with phalanx-type growth are more successful in competitive environment (Schmid & Harper 1985, Humphrey & Pyke 1998). Considering competitive superiority of phalanx species it would be reasonable to expect that mobility of species should increase with increasing species richness.

Indeed, in some other studies the high mobility of shoots was related to high species richness (Sykes et al. 1994, Pärtel & Zobel 1995, van der Maarel & Sykes 1997). Also, Herben et al. (1997b) have suggested that high ramet turnover rates may promote coexistence of a large number of plant species. Contrary to that conclusion, Klimeš (1999) found very low shoot mobility in species-rich grassland, which indicates that many species either kept their positions over many years or established in micro-sites that had previously been occupied by ramets belonging to the same species.

From clonal growth point of view, it is the decrease of average ramet life span in community that leads to increase in speed of ramet turnover. However, it is not appointed here, whether the ramets are replaced by conspecific ramets or by ramets of other species. I believe that the well-documented and fast turnover of shoots in species-rich communities (van der Maarel & Sykes 1993) may be as fast and as common also in species poor communities (see also Herben et al. 1994, Klimeš 1999). It is just "hidden" behind the replacement of ramets by conspecifics which, mostly, can not be detected by counting the shoots only. Many tussock-forming plants have annual ramets (e.g. *Molinia caerulea*, *Deschampsia caespitosa*) and thus high ramet turnover speed. Still, their high capability for vegetative reproduction and small length of rhizome branches make them very resistant to

invasions, strong patch-holders and therefore commonly dominants in undisturbed meadows. Thus, one can observe decreasing vegetative mobility and increasing shoot turnover both coinciding with decreasing species density in open meadows. However, productivity of the system, relative importance of competitive interactions, and spatial heterogeneity also influence the patterns of clonal growth and ramet turnover in the community.

CONCLUSIONS

From the studies performed and presented in this thesis I found that, indeed, competition intensity increases with increasing productivity of the community. In clonal plants the effect of competition is mostly related to reduction in reproductive success. The effect of competition on survival of individual genets and size of ramets is not as large as the effect on reproduction. Rhizomes and other perennating organs provide enough resources for growth and survival of a few ramets. However, when the neighbouring plants are competitively superior, they reduce the amount of gained assimilates for target ramets to the level when the latter don't have enough resources to produce offspring. In perennial plants survival comes first, and only if that is met also reproduction and expansion are possible. Thus, in clonal plants competition directly affects population dynamics.

There are three main characteristics of clonal propagation that largely determine population dynamics of clonal plants. These are speed of vegetative reproduction, life span of a ramet, and speed of vegetative (clonal) mobility. I found that the way these three parameters, when averaged over all species in the community and weighed with abundance of species, change in response to changes in environment is community-specific. This is especially true for vegetative mobility. In some cases species that are excluded from community when competition increases (e.g., due to fertilization of a wooded meadow) possess similar capability for mobility as species that become dominant. In case of open meadows decreasing species density (due to increase in competition intensity) is associated with decrease of clonal mobility as competitively dominant tussock-forming species take over. In case when cover of trees creates heterogeneity of light conditions and succession towards forest may be fast, species with long mobility and, thus, with ability to search for gaps (i.e. forage for light) gain in abundance.

In general, increase in productivity brings about an increase in speed of turnover of ramets. This is mainly due to decreasing average ramet life span in the community, but in some cases it also is associated with increase in speed of clonal mobility and vegetative propagation. Most interestingly, there appears to be a strong positive correlation between species richness of a community and ramet life span in open meadows, suggesting negative correlation between species richness and ramet turnover speed. One can now conclude decrease in time two ramets are neighbouring, and, thus, interact when intensity of competition increases and species richness decreases. Yet again, however, this is a community-dependent result being exactly opposite in wooded meadows. However, in wooded meadows the change of species density probably is not related so much to the changes in competitive interactions but to changes in light conditions. Thus, when the probability of competitive exclusion increases with productivity then a consequent effect is dominance of stronger tussock species and decreasing number of coexisting species both along experimental and natural productivity gradients.

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SUMMARY IN ESTONIAN

Konkurents ja kooseksisteerimine klonaalsetel taimedel erineva produktiivsusega kooslustes

KOKKUVÕTE

Jah, ma tean, et pole midagi erilist. Kõik on nii hästi-halvasti, kui alati on olnud. Sajandeid, tuhandeid.

Paljud on ju väga ühtmoodi asju öelnud. Igasugu kirjanikud. Aga mõistus – see on vaid kriitika. Ja vastused on väljamõeldised.

Peeter Sauter

Käesolev doktoritöö võtab kokku uuringud, mis käsitlevad liikidevahelisi suhteid klonaalsetel taimedel ning nende mõju koosluse struktuurile ning liigilise koosseisu dünaamikale. Erilise vaatluse all on muutused tehislikel ja looduslikel produktiivsusgradientidel, sest varasemad uuringud on teravalt tõstatanud küsimused, kas konkurents intensiivistub koosluse produktiivsuse tõustes ja kuivõrd see mõjutab koosluse liigirikkust?

Klonaalsed taimed on oma paljunemisviisidelt, populatsioonidünaamikalt ja ökoloogialt väga mitmekesised. Ka koosluste arengut mõjutavad nad mitmeti. Nii on kõige liigirikkamates kooslustes enamuses just klonaalse paljunemisviisiga taimed ja püsiktaimed. Mitmed haruldased ja alati vähearvukad liigid on peamiselt vegetatiivse uuenemisega. Samas hakkavad neis kooslustes, kus liigirikkust soosiv ekstensiivne majandustegevus katkeb, domineerima ja teisi liike välja tõrjuma samuti vegetatiivselt uuenevad liigid.

Looduslikes taimekooslustes sõltuvad interaktsioonid taimede paiknemisest ruumis. Omavahel interakteeruvad vaid need isendid, kes paiknevad selleks küllalt lähestikku. Vegetatiivse uuenemise mehhanism määrab järglaste paigutumise ruumis ja annab taimedele võimaluse teatud määral ka oma järglastele soodsamaid laike valida. Kolm peamist tunnust, mille varieerumine määrab taimede klonaalsete järglaste hulga, paigutumise, ja seega ka populatsioonidünaamika ning koosluse horisontaalse struktuuri, on taimede vegetatiivne liikuvus, vegetatiivse uuenemise kiirus ja rameti eluiga.

Liikuvus, mis on määratud rameti risoomiosa ja/või stooloni pikkusega, ning uuenemise kiirus, mis on ühe rameti järglasrametite arv teatud ajaühikus, määravad taimede levimise ruumis. Rameti eluiga omakorda määrab mingi ruumiosa hõivamise aja ja seega ka rametite vahetumise kiiruse. Suure töömahu tõttu on seni

tehtud vaid üksikuid uurimusi võrdlemaks loetletud tunnuseid erinevate koosluste vahel kogu koosluse liigilise koosseisu tasemel. Veelgi vähem on töid, kus oleks mõõdetud, kas koosluses keskmiselt vegetatiivse uuenemise parameetrid muutuvad olulisemate keskkonnatunnuste muutudes. Sellised uuringud võimaldavad hinnata erinevate klonaalse kasvu vormide edukust erinevais tingimustes ning klonaalse kasvu mõju populatsioonide ja koosluste dünaamikale. Käesolevas doktoritöös olen püüdnud seda lünka täita.

Kasutades taimede klonaalse kasvu kohta kogutud andmeid Laelatu puisniidult (Läänemaa) ning sealsamas erineva valgustatusega (erineva puurinde liituvusega) kooslustes tehtud taimkatteanalüüse arvutasin ma iga taimeruudu jaoks kõigi kolme klonaalse kasvu tunnuse kaalutud keskmise. Kaaluna arvestasin analüüsiruudul kasvanud soontaimeliikide katvust. Osutus, et kui uuritud kooslused jaotada kolme laia tüüpi: mets, puisniit ja lage niit, siis erines klonaalse kasvu vormide jaotus nende tüüpide vahel märgatavalt. Isegi klonaalse kasvu tunnuste kaalutud keskmiste (näiteks vegetatiivse liikuvuse) ja keskkonnatunnuste (näiteks produktiivsuse) vahelised seosed erinesid erinevais kooslusetüüpides.

Ootuspäraselt erineb niidukooslustest metsa alustaimestiku kasvuvormiline koosseis. Rohttaimed, mis võivad metsas arvukalt esineda on suure vegetatiivse liikuvusega ja sageli ka pikaealiste rametitega. Kuivõrd metsa alustaimestiku jaoks on kõige olulisem valguse kättesaadavus, siis on suur liikuvus oluline omadus, et leida kasvuks sobivaid laike. Madal rametite tihedus omakorda viitab, et konkurentsisuhted ei ole rohttaimede vahel kuigi olulised. See annab võimaluse leitud laiku pikaajaliselt asustada.

Lagedates niidukooslustes on keskkonnatingimused oluliselt homogeensemad, rametite tihedus palju suurem ning (eriti niitmise ja/või karjatamise puudumisel) konkurents selgelt tugevam. Sellistes kooslustes on suur liikuvus eeliseks vaid siis, kui uus asustatav laik paikneb nõrgemate konkurentide naabruses. Oluliselt edukam aga on faalanks-kasvuvorm. Faalanks-taimed asustavad uusi alasid aeglaselt ja liiguvad ruumis vähe, ent on sealjuures väga vastupidavad hõivatud ala hoidmisel. Võrreldes metsadega erineb niitudel juba asustatud laigu hoidmise mehhanism. Selgelt väheneb selliste liikide osakaal, kellel on pikaealised rametid ja nende asemel hakkavad domineerima üheaastaste rametitega liigid, kes paigutavad oma järglased emarameti lähedusse. Tugevama konkurentsi tingimustes on eelis mättana kasvavail liikidel, millistest paljud on lühiealiste rametitega.

Nii Eestis, Laelatu puisniidul ja selle ümberkaudsetes kooslustes, kui Põhja-Norras Finnmarkis kahe erineva taimeliigiga läbi viidud katsed näitasid selgelt, et konkurentsi intensiivsus koosluse produktiivsuse kasvades tõuseb. Klonaalsetel taimedel ei ole aga konkurentsi mõju tuvastatav niivõrd üksiku rameti kasvu vähenemisena, kuivõrd kogu geneti kasvu vähenemisena. Suuresti avaldub see vegetatiivsete järglaste arvu vähenemisena. Mitmeaastased taimed saavad paljunemist ressursside puudumisel edasi lükata ja sel viisil kindlustada genetite eluspüsimist. Geneti ellujäämine on aga eeldus paljunemisvõimaluse säilitamiseks tulevikus.

Väga tavaline on taimeökoloogilises kirjanduses väide, et liigirikkuse vähenemine produktsioonigradiendil toimub taimedevahelise konkurentsi intensiivsuse kasvamise tõttu. Üllatavalt väike on aga selle väite kohta esitatavate tõendmaterjalide hulk. Siin töös leitud erinevused Eesti ja Norra taimekoosluste vahel näitavad, et koosluse liigirikkus väheneb produktsiooni kasvades kui samal ajal kasvab konkurentsi intensiivsus. Samas, selleks, et madalama produktiivsusega kooslustes saaks konkurentsi vähenedes liikide arv kasvada, on vajalik suhteliselt suure liigifondi olemasolu. Liigifond seab ülempiiri maksimaalsele liigirikkusele koosluses, olles ise samal ajal tehniliselt sõltuv ümberkaudsetel aladel konkurentsitingimustes püsima jäänud liikide arvust. Lokaalselt määravad kooseksisteerivate liikide arvu aga ikkagi liikidevahelised suhted, mis võivad olla võimendatud või leevendatud koosluse ajaloo poolt, näiteks niitmise sageduse poolt rohumaadel.

Kui liikide arvu vähenemine koosluses on põhjustatud konkurentsist, siis tähendab see ühtlasi, et tugevaim konkurent hakkab koosluses domineerima. Oleks ootuspärane arvata, et sellistel dominantidel on mingeid kindlaid ühisjooni ka vegetatiivse paljunemise osas, kuivõrd nad peaaegu alati on klonaalsed liigid. Käesoleva töö tulemuste järgi võib väita, et selliseks ühisjooneks on eelkõige faalanks-kasvuvorm. Muutusi üksikute vegetatiivse uuenemise tunnuste kaupa vaadeldes aga selgeid ja üheseid tendentse ei ole. Näiteks Laelatu väetuskatses kasvasid keskmine liikuvus ja paljunemiskiirus töötlustes, mis kannatasid kõige suurema lämmastikupuuduse käes ja kus seetõttu domineerisid liblikõielised. Samas domineerisid kõrgeima lämmastiku kättesaadavuse juures liigid, mis ei erinenud oma klonaalse kasvu tunnustelt väetamata kontrollruutudel kasvavatest ja samast töötlusest välja tõrjutud liikidest.

Nii teoreetilistes töödes kui ka mõningates katsetes on näidatud, et liikide kooseksisteerimine on tõenäolisem kui liigid on oma liikuvuselt selgelt erinevad. Käesolevas töös sellele väitele kinnitust leida ei õnnestunud. Teisalt on mitmetes töödes leitud, et liigirikastes kooslustes toimub kiire võsude vahetumine. Nähtus, mis on tuntud ka "liikide karussellina", annab aluse väita, et pikema aja jooksul võib peaaegu iga liik koosluses asustada peaaegu iga mikrolaigu, andes seal elanud rameti surma järel selle jälle vabaks mõne teise rameti jaoks, olgu see siis samast liigist või mõnest teisest. On ka väidetud, et selline rametite vahetumine võib kaasa aidata liigirikka koosluse kujunemisele, kuna suurema ringe kiiruse juures väheneb aeg, mil kindlate liikide isendid, sealjuures ka nõrk konkurent tugeva konkurendi kõrval, kõrvuti kasvavad ja konkureerivad. Ent viimase väite võib ka teistpidi pöörata. Mida tugevam on konkurent, seda lühemat aega saab tema kõrval nõrgem taim kasvada. Ja mida suurem on konkurentsivõimete erinevus või üldine difuusse konkurentsi tase, seda kiiremini nõrk taim välja tõrjutakse. Minu tulemused kinnitavad, et just viimane mehhanism võiks toimida Lääne-Eesti lubjarikastel rohumaadel. Tõik, et produktiivsuse kasvades väheneb pikaealiste rametitega liikide osakaal koosluses, viitab otseselt sellele, et rametite ringekiirus suureneb. Et samal ajal kasvab tõesti ka konkurentsi intensiivsus, näitavad otsesed konkurentsi

mõõtmised. On oluline teha vahet rametite vahetumisel, mida ei ole sageli, eriti liigivaestes kooslustes, võimalik tuvastada vaid võsude vahetumist jälgides, ning vegetatiivsel liikuvusel. Minu tulemused viitavad sellele, et rohurinde produktiivsuse kasvades neist esimese kiirus koosluses keskmiselt suureneb ja teine väheneb.

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PUBLICATIONS

I

The deadly missile attack shortly to be launched by an ancient automatic defence system will result merely in the breakage of three coffee cups and a micecage, the bruising of somebody's upper arm, and the untimely creation and sudden demise of a bowl of petunias and an innocent sperm whale.

Douglas Adams

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Competition intensity and its importance: results of field experiments with *Anthoxanthum odoratum*

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Abstract The effect of community productivity on competition was studied in 82 permanent plots using two removal experiments with the rhizomatous perennial grass *Anthoxanthum odoratum*. The removal of neighbouring plants had a positive effect on the number of shoots and total above-ground biomass of *Anthoxanthum* but no significant effect on mean shoot biomass. The relative competition intensity coefficient (RCI) calculated from these data showed that competition intensity increased with increasing community productivity. Similarly, the importance of competition and the difference between local maximum and local average population density increased with increasing community productivity. We concluded that for *Anthoxanthum* the impact of competition is greater in high-productivity areas and that competition reduces population density. No evidence was found supporting the importance of positive interactions between plants in tundra areas.

Key words Importance of competition · Productivity Removal experiments Tundra Wooded meadow

Introduction

Although there have been a number of experiments analysing the relationships between competition intensity and major community parameters (Putwain and Harper 1970; Silander and Antonovics 1982; Berendse 1983; Keddy 1989; Aerts et al. 1990; Di Tomasso and Aarssen 1991; Wilson and Tilman 1991, 1993; Gerry and Wilson 1995; Kadmon 1995; Herben et al. 1997; McLellan et al. 1997), there is as yet no general agreement on how competition changes along the principal natural gradients.

Three main hypotheses about variation of competition intensity along the productivity gradient state that either (1) competition intensity increases with increasing productivity (Grime 1973, 1979); (2) total competition intensity does not change with community productivity, but shifts from the below-ground environment in low productivity communities to the above-ground environment in high productivity environments (Newman 1973; Tilman 1982, 1988); or (3) competition intensity is minimal in plant communities of low (but not the lowest) productivity (Fretwell 1977; Oksanen 1990, 1993).

While competition intensity has received a great deal of attention, the importance of competition has remained almost unstudied. The importance of competition is defined as the relative impact of competition, among other processes, on the community composition or population dynamics (Welden and Slauson 1986; Goldberg 1994). Measurement of the importance of competition requires population-level studies in natural conditions. However, most competition research has been carried out on the level of the individual plant, or competition characteristics have been estimated from the parameters of individual plants.

Although the importance of competition is not a simple concept, the distinction between this and competition intensity has been clearly defined (see Welden and Slauson 1986). In principle, the importance of competition can be measured by four methods:

1. All major local factors that affect community composition are studied separately and compared to real community structure. From this, the relative impact of competition will be calculated. This method requires a very large number of experiments and its use is unrealistic in natural conditions.
2. Goldberg (1994) proposes a method by which the dynamics of an unmanipulated natural community is

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compared to the dynamics of each single species of this community when grown separately from the others, i.e. with the dynamics of the monocultures of all species present in this community. Using monoculture densities, the "null community" is calculated and compared to the natural community (see Goldberg 1994 for details). The approach requires monocultures of each species as well as an additive mixture of all species to be established. This means that if a community consisted of e.g. 20 species, the method would involve 21 treatments, which makes it extremely labour-consuming.

3. Welden and Slauson (1986) used the relative amount of variation in experimental data caused by removal of competition as a measure of the importance of competition. This is a simple method which has unfortunately not been widely used.
4. We propose that the difference between mean real population density and maximum potential population density in a certain community be used as an estimate of importance of interspecific competition. This method is simpler than that proposed by Goldberg (1994), while its results do not apply to the whole community but only to the species studied, as does also the method suggested by Welden and Slauson (1986).

In this paper we will use the data from two very similar experiments performed in different geographical regions with the aim of studying the variation of both the intensity and importance of competition along a productivity gradient.

Methods

Experimental design

The data from two experiments on the perennial grass species *Anthoxanthum odoratum* (further referred to as *Anthoxanthum*), conducted in Estonia and in Norway, were included in this analysis. *Anthoxanthum* is a common plant in both study areas, and reproduces well both sexually and vegetatively. Its ramets (*sensu* Harper 1977) are mainly annual, although they sometimes survive for 2 years. The mean number of rhizome branches per ramet is 0.86 (maximum 9), mean speed of vegetative reproduction (ramets ramet^{-1} year^{-1}) 0.5 (with a maximum of 4.5) and mean annual rhizome branch growth 4.5 mm (maximum 25 mm). There was no significant difference between the two study areas in the clonal growth pattern of *Anthoxanthum*.

The first experiment was conducted at Laelatu wooded meadow and its neighbouring meadow communities on the western coast of Estonia (58°35′15″N, 23°34′00″E). The area is a part of the Laelatu-Puhtu-Nehatu Nature Reserve. All communities studied were calcicolous grasslands. The area belongs to the boreo-nemoral zone. The mean temperature for July is 17.0°C and for January –5.0°C; the mean annual precipitation is 500 mm. A more detailed description of the site is given by Kull and Zobel (1991).

The second experiment was conducted in northern Norway, at Joatkajav'ri fjellstue, on the lower part of the Finnmarksvidda plateau (69°46′, 23°58′), at about 400–600 m above sea level (a.s.l.). This area includes tundra meadows, lichen heaths, willow thickets and birch forests, although most of the area is devoid of trees. The mean annual precipitation is 450 mm, and the mean temperature for July is 10°C and for January –10°C. A more detailed description of this area is given by Moen (1993). Some characteristics of the communities studied are given in Table 1.

In Estonia, three herb communities of different productivity and similar light conditions were chosen. Before the experiment

Table 1 Characteristics of studied communities

Community	Country	Mean aboveground phytomass (g m^{-2})	Mean number of species per:		Elevation above sea level (m)	Main dominant plant species
			1 m^2	400 cm^2		
Low-productivity wooded meadow	Estonia	700	32		3.5	*Scorzonera humilis, Hepatica nobilis, Sesleria caerulea, Festuca rubra, Carex ornithopoda, C. flacca, Convallaria majalis*
Medium-productivity wooded meadow	Estonia	900	37		3	*Hepatica nobilis, Brachypodium pinnatum, C. majalis, Plantago lanceolata, Primula veris, Serratula tinctoria, Briza media*
Abandoned hayland	Estonia	1,100	28		1.5	*Dactylis glomerata, Festuca rubra, Helictotrichon pratensis, Brachypodium pinnatum, Primula veris, Carlina vulgaris, Carex tomentosa*
Snow-bed	Norway	310		8	620	*Salix herbacea, S. polaris, Vaccinium myrtillus*
Willow heath	Norway	430		11	520	*F. rubra, V. myrtillus, Juniperus communis, Betula nana, Empetrum nigrum*
Birch forest	Norway	360		13	480	*V. myrtillus, Trollius europeaus, F. rubra, Trientalis europea*
Herb-rich meadow	Norway	620		14	475	*Trollius europeaus, V. vitis-idea, Cirsium heterophyllum, Epilobium angustifolium*
Clearing in birch forest	Norway	650		10	460	*Cornus suecica, Solidago virgaurea, Trientalis europea, Deschampsia flexuosa*

all sites had been irregularly mown. During the experiment no mowing was done. In each community, two sites with eight permanent 30×30 cm plots (2 manipulated and 2 control plots at each site) were established.

In Norway, five communities were selected along the altitudinal gradient on a hill slope with southern exposure, within a vertical range of about 160 m (460–620 m a.s.l.). In each community, two sites with 12 permanent 20×20 cm plots (3 manipulated and 3 control plots at each site) were established, except for the lowermost community which was smaller in size and included 5 manipulated and 5 control plots.

In both experiments, the same manipulation methods were used for measurement of total competition (i.e. combination of above- and below-ground competition). In manipulated plots, the above-ground parts of all species, except for *Anthoxanthum*, were removed several (3–5) times in all seasons from 1993 to 1995. During the 1st month of the experiment, regrowth of clipped plants was quite intense. From the 2nd month their sprouting decreased remarkably and from the middle of the 2nd year of experiment it was minimal (for species other than *Anthoxanthum* approx. 2–3 shoots per plot per month). This allowed the conclusion that most below-ground parts of clipped plants had died or stopped functioning, and hence also below-ground competition was reduced. To minimise below-ground immigration of competitors from neighbouring areas, the roots were trenched to the depth of the whole humus layer (max. about 25 cm) along the edges of both manipulated and control plots with the same frequency as the clipping of above-ground parts. In most cases in Norway, trenching approached base rock, while in Estonia the depth of trenching corresponds to a depth which includes at least 95% of all roots of the herbal community (K. Kull, unpublished work). Trenching of the edges of control plots was applied in such a way as to reduce the side effects of trenching (e.g. response of *Anthoxanthum* to root damage) on experimental data.

In each plot the number of shoots was counted twice a year – at the end of June and at the end of August (except June 1994 when the number of shoots was counted only in Norway). At the end of the experiment the above-ground parts of plants were collected from all plots. The biomass obtained from control plots was separated into two fractions – "*Anthoxanthum*" and "other species" The samples were dried at 80°C for 48 h, and weighed to an accuracy of 0.01 g.

To estimate the productivity of the direct neighbourhood of target plants, the above-ground plant parts of the field layer (including litter) were collected at the time of maximum living biomass (at the end of June in Estonia and in August in Norway) in the first 2 years of the experiment (1993, 1994) from four samples of 10×30 cm per community outside the permanent plots. The samples were dried at 80°C for 48 h and weighed to an accuracy of 0.1 g. In Norway the number of species was counted in each control plot in June 1993 and in Estonia in two 1 m^2 plots in each community in June 1993.

Data analysis

Both data sets were standardised so that the number of shoots and biomass of *Anthoxanthum* could be presented per 1 dm^2.

Relative competition intensity was calculated for the number of shoots as:

$$RCI_N = (N_m - N_c)\,N_m^{-1}, \quad (1)$$

where N_m is the number of shoots in manipulated plots at the end of the experiment and N_c is the number of shoots in control plots at the end of the experiment.

Relative competition intensity was also calculated for the total biomass of *Anthoxanthum* per plot:

$$RCI_W = (W_m - W_c)\,W_m^{-1}. \quad (2)$$

Here W_m is the total biomass of *Anthoxanthum* in manipulated plots at the end of the experiment and W_c is the total biomass of *Anthoxanthum* in control plots at the end of the experiment.

Table 2 Shoot densities at the beginning and end of the experiment, and total above-ground phytomasses and shoot weights of *Anthoxanthum* at the end of the experiment, in different communities and different treatments (mean±SD) (t t-statistic for comparison of the difference between initial and final densities, P probability level)

Community	Number of shoots per dm^2							Above-ground phytomass of *Anthoxanthum* (g dm^{-2})		Mean shoot weight of *Anthoxanthum* (g)	
	Manipulations				Controls						
	Beginning	End	t	P	Beginning	End	t	P	Manipulations	Controls	Manipulations	Controls
Low-productivity wooded meadow	0.61±0.3	5.9±2.9	-3.5	0.039	0.67±0.37	0.3±0.1	3.67	0.03	0.17±0.1	0.01±0.01	0.03±0.016	0.025±0.016
Medium-productivity wooded meadow	1.22±0.7	9.64±1.4	-15.8	0.001	0.83±0.38	2.5±3.3	-1.12	0.35	0.3±0.11	0.05±0.06	0.031±0.014	0.03±0.03
Abandoned hayland	2.3±1.9	12.0±1.7	-244	0.000	0.56±0.33	2.1±2.1	-1.62	0.20	0.43±0.09	0.14±0.2	0.04±0.012	0.04±0.03
Snow-bed	22.5±9	30.7±13	-1.69	0.15	17.8±7.18	17.7±8	0.09	0.93	0.7±0.3	0.4±0.2	0.023±0.003	0.024±0.005
Willow heath	12.9±5.3	18.8±5.2	-4.36	0.007	11.4±7.7	9.9±4.7	0.73	0.49	0.36±0.19	0.25±0.12	0.018±0.005	0.028±0.013
Birch forest	10.9±8.6	15.3±8.9	-4.71	0.005	12.1±3.6	11±3.8	0.69	0.52	0.46±0.29	0.35±0.16	0.03±0.01	0.032±0.01
Herb-rich meadow	9.6±4.4	16.3±7.2	-3.02	0.03	8.0±1.9	11.0±6	-1.33	0.24	0.38±0.2	0.46±0.38	0.024±0.008	0.038±0.012
Clearing in birch forest	10.0±5.8	15.4±5.5	-3.13	0.035	7.8±2.4	4.6±3.2	2.1	0.1	0.05±0.27	0.17±0.18	0.035±0.13	0.027±0.024

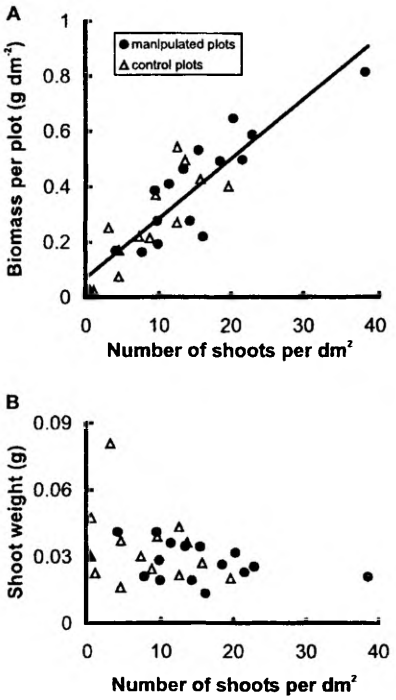

Fig. 1 **A** Total biomass of *Anthoxanthum* per plot and **B** mean shoot weight of *Anthoxanthum*, in relation to the number of shoots of *Anthoxanthum* per plot in both manipulated (*filled circles*) and control plots (*open triangles*) at the end of the experiment. Plotted trendline (y=0.02x+0.07, r^2=0.78) is statistically significant at P<0.05. Note that there is no difference between manipulated and control plots in biomass vs. number of shoots relationship

Also, relative competition intensity was calculated for the mean shoot weight of *Anthoxanthum*:

$$RCI_{WS}=(WS_m-WS_c)\,WS_m^{-1}. \quad (3)$$

Here WS_m is the mean shoot weight of *Anthoxanthum* in manipulated plots at the end of the experiment and WS_c is the mean shoot weight of *Anthoxanthum* in control plots at the end of the experiment.

Importance of competition (IC) in a community for the number of shoots was calculated from the results of multivariate analysis of variance, as proposed by Welden and Slauson (1986). The relative importance of competition is the percentage of variation, accounted for by treatment effect, which equals to the sum of the squares of deviations, due to removal of neighbouring plants (SS_{factor}), divided by the total sum of the squares of deviations (SS_{total}):

$$IC=SS_{factor}\,SS_{total}^{-1}. \quad (4)$$

The difference between maximum population density and mean population density in a particular community (R) was calculated as:

$$R=N_{max}N_{cmean}^{-1}. \quad (5)$$

Here N_{max} stands for maximum shoot density found within a given community, and N_{cmean} is overall mean shoot density for the same community in control plots throughout experiment.

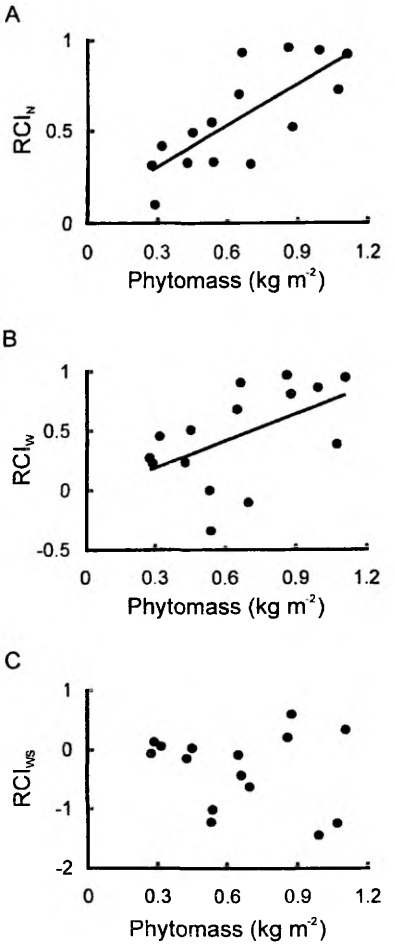

Fig. 2 Relationships between the coefficients of relative competition intensity (*RCI*) and above-ground community phytomass for coefficients calculated from **A** number of shoots of *Anthoxanthum* per plot (RCI_N), **B** total biomass of *Anthoxanthum* per plot (RCI_W), and **C** mean shoot weight of *Anthoxanthum* (RCI_{WS}). Only statistically significant *trendlines* (at P<0.05) are plotted: **A** RCI_N= 0.0008x+0.08, r^2=0.58; **B** RCI_W=0.0008x–0.04, r^2=0.27

Since calculation of importance of competition involved analysis of variance, it was calculated on a per-community basis. All other coefficients were calculated on a per-site basis. To compare IC to R and RCI_N, the last two parameters were averaged over the community.

The data were analysed using the program STATISTICA (StatSoft 1995). Before analysis, all data were log-transformed. To determine treatment effects on the number of shoots and biomass of *Anthoxanthum* the nested subset ANCOVA was used, with community (8 different communities) nested in geographical region (Estonia and Norway). Site was not used as a factor in order to keep the number of replicates on a reasonable level. All factors were treated as fixed factors. Initial shoot density of *Anthoxanthum* per plot was used as a covariable.

A t-test for dependent samples was used to compare initial and final shoot densities. Regression analysis was applied to estimate the relation of competition parameters to community productivity.

Results

Shoot numbers increased significantly in the manipulated plots of all communities studied except for the snow-bed (Table 2). More than 90% of new shoots in the plots were of vegetative origin. The only significant change in shoot numbers in control plots was observed at the low-productivity wooded meadow site, where the number of shoots decreased by 50% (Table 2).

Overall treatment effect was significant for the shoot numbers and total biomass of *Anthoxanthum* per plot, but not for the mean shoot weight of *Anthoxanthum* (Table 3). Per-plot analysis showed a significant correlation between the shoot density and total above-ground biomass of *Anthoxanthum* (Fig. 1A). Removal of other plants had no effect on this relationship. No relationship was detected between shoot density and mean shoot weight either in manipulated or control plots (Fig. 1B).

There were three communities for which treatment had no effect on shoot numbers. All these communities – snow-bed, birch forest and herb-rich meadow – were in Norway. Treatment effect on the total above-ground biomass of *Anthoxanthum* per plot was significant only at the low- and medium-productivity wooded meadow sites in Estonia and in a birch forest clearing in Norway. The only site with a significant response in per-shoot biomass to removal of other plants was the herb-rich meadow in Norway.

Both RCI_N and RCI_W were positively correlated with above-ground community phytomass (Fig. 2). RCI_{WS} had no significant relation to community phytomass. IC and R were also positively correlated with above-ground community phytomass (Fig. 3). The best fit for R was exponential. IC and RCI_N were linearly positively correlated (Fig. 4A). The relation of R to IC and RCI_N was also positive but non-linear (Fig. 4B,C).

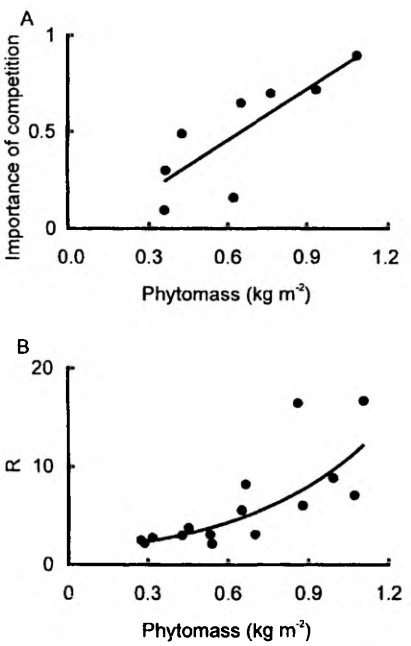

Fig. 3 The values of **A** importance of competition (IC) and **B** difference between maximum population density and average population density (R) in relation to community above-ground phytomass. Both *trendlines* are statistically significant at $P<0.01$: **A** $IC=0.0009x-0.074$, $r^2=0.67$; **B** $R=1.27e^{0.002x}$, $r^2=0.69$

Discussion

The few previous studies we could find in which importance of competition was measured in natural plant communities showed that competition is more important for smaller species (McLellan et al. 1997), and that intraspecific competition is more important than interspecific (Briones et al. 1996). The first result should apply more strictly to above-ground competition, where shading by bigger neighbouring plants is an influential process. The hypothesis of the greater importance of intraspecific competition compared with interspecific competition is, in theoretical works, often used as a criterion for coexistence (often called the Lotka-Volterra coexistence criterion; see e.g. MacArthur 1972; Leon and Thumpson 1975; Tilman 1982), and has also been confirmed in several experimental studies (e.g. Weiner 1980; Fowler 1982; Berendse 1983; Johansson and Keddy 1991). The third study addressing the importance of competition (Welden et al. 1988) established no relationship either between competition intensity and water stress, or between importance of competition and water stress for shrubs in northwestern Colorado. The effect of productivity on interactions between species was not studied directly in any of these papers, although water stress may be related to productivity.

Table 3 Effect of removal on shoot number and total biomass of *Anthoxanthum* per plot, and mean shoot weight of *Anthoxanthum* as tested by nested subset ANCOVA

		Sum of squares	*df*	Mean square	*F*	*P*
Shoot number	Effect	25.9	1	25.9	31.25	<0.0001
	Error	53.0	64	0.83		
Total biomass	Effect	23.6	1	23.57	76.88	<0.0001
	Error	19.62	64	0.31		
Shoot weight	Effect	0.054	1	0.054	0.19	0.66
	Error	18.27	64	0.285		

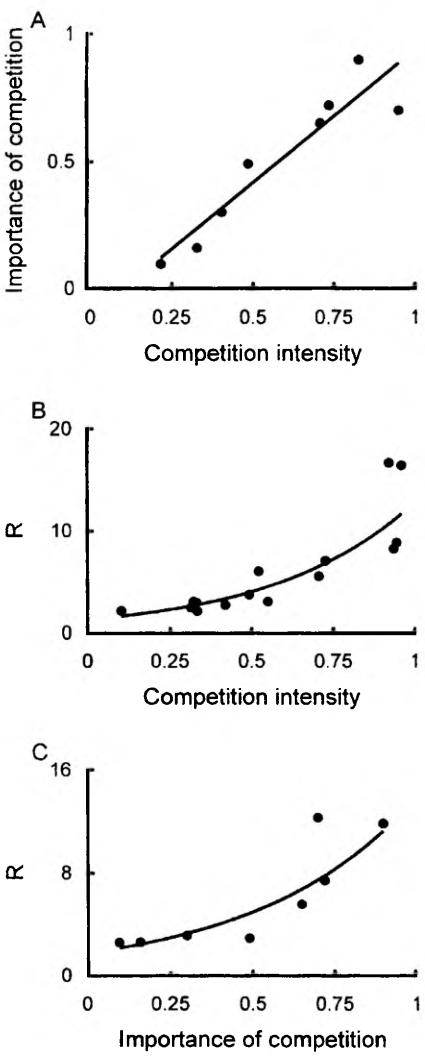

Fig. 4A–C Interrelationships between importance of competition (IC), difference between maximum population density and average population density (R), and relative competition intensity calculated from the number of shoots of *Anthoxanthum* (RCI_N). All *trendlines* are statistically significant at $P<0.01$: **A** $IC=1.05x-0.11$, $r^2=0.88$; **B** $R=1.30e^{2.28x}$, $r^2=0.85$; **C** $R=1.77e^{2.06x}$, $r^2=0.81$

We found in our experiment that importance of competition was higher at sites with higher productivity (i.e. at sites with larger neighbouring plants). We noted also increase in the intensity of competition with increasing productivity. This provides clear support for Grime's and Oksanen's hypotheses. It is important to keep in mind, however, that *Anthoxanthum* is a small plant and therefore expected to be more vulnerable to the presence of neighbours (Di Tomasso and Aarssen 1991; McLellan et al. 1997).

Following the hypothesis of Tilman (1988), species with low shoot/root ratios and low stature (like *Anthoxanthum*) are expected to suffer more in habitats of higher productivity even if the importance of competition remains constant, since productive habitats are characterised by more intense shoot competition. Therefore, we cannot really falsify Tilman's hypothesis. However, in our experiment we also reduced below-ground competition. Considering this, our results tend to support the idea of increase in overall importance of competition (i.e. combined above- and below-ground competition) with increasing primary productivity.

Previously, competition intensity has been shown both to increase with increasing community productivity (e.g. Wilson and Keddy 1986; Campbell and Grime 1992; Turkington et al. 1993; Bonser and Reader 1995; Gaudet and Keddy 1995; Kadmon 1995) or to have no relation to productivity (e.g. Welden et al. 1988; Di Tomasso and Aarssen 1991; Wilson and Shay 1990; Wilson and Tilman 1993; Cahill 1999). Our results show a clear relationship between community above-ground phytomass and competition intensity when the latter is calculated using population-level measures, such as number of shoots. We found no relationship between competition intensity and productivity when we used mean shoot biomass as a measure of plant performance. This confirms the recent idea that competition intensity should increase with increasing productivity when survival or community structure is assessed but not when growth of individuals is measured (Goldberg and Novoplansky 1997).

In general, intensity and importance of competition need not necessarily correlate (Welden and Slauson 1986). In our experiment this correlation was very strong (Fig. 4A). We hope to see some more publications with IC in the future to compare our results with others.

Use of R yields some interesting results, since it is much more sensitive than IC or RCI_N on high levels of competition intensity (Fig. 4B,C). Besides, R has a very distinct and clear biological meaning: it indicates decrease in population density due to competition. We suppose that R should be clearly different for dominants and subordinants, since the population density of the former is likely to be close to maximum, while the latter can benefit significantly from free space. Comparison of the values of R for different species within a community can therefore be used for elaboration of competitive hierarchies.

Our results show that decrease in population density due to competition increases in case of small species (like *Anthoxanthum*) with the increasing size of neighbouring plants. However, at the low-productivity end of the gradient, tall species may lose their advantage over small species, since they do not grow so big in those communities and therefore can not outcompete smaller species. This is in agreement with empirical data from species-rich communities which are characterised by small vegetation and low productivity (Grime 1973, 1979; Kull and Zobel 1991). If species richness is a community characteristic, then in species-rich habitats no

species can have high maximum population density, and, equally low values of *R* are expected for all species. If species richness is the result of ecological processes that reduce dominance, then high *R* is expected for potentially dominant species in species-rich communities and low *R* is expected for potentially subordinant species.

There has been a debate concerning the importance of positive interactions between plants, especially in arctic areas (Carlsson and Callaghan 1991; Callaway 1995, 1997, 1998). One of our experiments was carried out in a subarctic tundra area where positive interactions are assumed to be frequent (Bertness 1998). However, we found no support for the idea that *Anthoxanthum* might benefit from the presence of other species even in very harsh, windy and water-stressed snow-bed habitats. This corresponds to the results obtained for *Oxyria digyna* and *Ranunculus glacialis* (Olofsson et al. 1999).

There were enough shoots in the plots to expect occurrence of intraspecific competition. *Anthoxanthum*, indeed, has high dependence on intraspecific interactions (Berendse 1983). However, if strong intraspecific competition had occurred in our experiments, we should have discovered a strong negative correlation between the shoot density and mean shoot weight of *Anthoxanthum*. We found no such relationship (Fig. 1B), and hence, there was no evidence of the density-dependence of the population dynamics of *Anthoxanthum* in our plots.

Theoretically, the behaviour of below-ground biomass in our experiments may have been different from that of above-ground biomass. Therefore, our results could have been different, if we had measured also the below-ground biomass of *Anthoxanthum*. It is known that allocation is very flexible and removal of neighbours directly affects the ratio of red to far-red light, which is a strong determinant of the carbon allocation pattern (Fitter and Hay 1987; Ridge 1991; Larcher 1995). After removal of neighbours, the allocation pattern is expected to shift more to below-ground organs. However, *Anthoxanthum* has very short, thin rhizomes that cannot store large amounts of assimilates. Since our experiment lasted three seasons, we can also assume that there was enough time for allocation to shoots to take place.

Another issue related to the below-ground environment is that in fact we have no way to estimate how effective the reduction of below-ground competition was. Considering that there may be several ways in which above- and below-ground competition interact (Cahill 1999), the different success of their exclusion may have a strong influence on results. However, given that very few non-*Anthoxanthum* individuals emerged in our manipulated plots during the last 1.5 years of the experiment, and that all of them were removed, it is not likely that many plants survived 3 years of continuous removal of assimilating tissues. Even if their roots and rhizomes survived, their life processes (including their role in competition) must have been considerably suppressed, otherwise we would have recorded the appearance of new small shoots. The method used in this work for reducing total competition (i.e. clipping plus regular trenching) has been regarded as one of the best ways of achieving this aim (Aarssen and Epp 1990), and it proved effective during our earlier experiments.

Our results emphasise the importance of demographic competition studies, since the response of shoot number in the plot (population density) to the removal of neighbours was much stronger than that of above-ground biomass which is usually considered the best measure of plant performance. Thus we can state that at least for *Anthoxanthum*, the primary effect of competition is not a decrease in biomass but a decrease in population density due to reduction in reproductive success.

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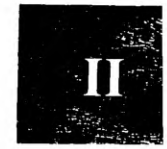

Kui sõnastan ma võõraid mõtteid
Ja mõtestan ma omi sõnu
Siis omastan ma võõraid võtteid
Ja loojatundest tunnen mõnu
Ning tunnetades ühtseid mõtteid
Loon ühtsustundest vastandsõnu

Tõnu Trubetsky

Sammul, M., Oksanen, L., Mägi, M.
Competition intensity, productivity and species richness:
a field experiment in two distant regions.
Manuscript.

COMPETITION INTENSITY, PRODUCTIVITY AND SPECIES RICHNESS: A FIELD EXPERIMENT IN TWO DISTANT REGIONS

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ABSTRACT

We studied the effect of productivity on competition intensity and the relationship between competition intensity and community species richness, using a removal experiment with the perennial plant *Solidago virgaurea*. The experiment was conducted in 16 different communities from two geographically distant areas (western Estonia and northern Norway). Removal of neighbours had a positive effect on the biomass of genets of *Solidago*. Total biomass of manipulated plants increased with increasing community productivity, whereas no such trend was detected for control plants. The corrected index of relative competition intensity, *CRCI*, increased with increasing community productivity. There was an indication that regional differences contribute to the productivity-competition relationship. Species richness was negatively correlated with *CRCI* in Estonia but not in Norway and not in the case of the pooled material. The results show that competitive exclusion operates at least in these communities which species pool is large.

The observed relationship between competition intensity and primary productivity is intimately connected to a concordant variation in the intensity of grazing. The least productive communities both in Estonia and in Norway are characterised by intensive grazing which reduces importance of competiton. Hence, the contrast corroborates the predictions of the Hypothesis of Exploitation Ecosystems, predicting that trophic dynamics account for the relationship between competition intensity and primary productivity.

We discuss a possible reason for the controversy concerning the relationship between primary productivity and the intensity of competition which may lie in the different successional status and pattern of distribution of studied habitats. Most studies conducted in North America are carried out on old-fields where low-productivity sites are embedded in the matrices of productive humid-temperate landscapes. Conversely, most Eurasian studies have been conducted

in large-scale natural or semi-natural communities which have been subject to grazing for centuries and have adjusted to it. Productivity-driven differences in the dynamics of the endotherm branches of grazing chains can only be expected to occur in productivity gradients of the latter type.

Key words: arctic, competition intensity, herbaceous plants, grasslands, productivity, removal experiment, *Solidago virgaurea*, species richness, temperate.

INTRODUCTION

For a couple of decades, plant ecologists have intensely debated whether there is a positive relationship between productivity of plant communities and intensity of competition. Several authors working on alpine and grazing-created heaths of northern and western Europe claim that such a connection exists, either directly (Grime 1979, Campbell and Grime 1992, Callaghan and Emanuelsson 1985, Carlsson and Callaghan 1991), or because herbivory is more intense in unproductive environments, where modest grazer densities suffice to generate intense grazing pressure (Fretwell 1977, Oksanen et al. 1981, Oksanen, L. 1990, Louda et al. 1990, Oksanen and Ranta 1992, Frazer and Grime 1997). The other main position is that the total intensity of competition does not depend on primary productivity, but competition shifts from shoot to root environments along gradients of decreasing primary productivity. This conjecture, which originally addressed the patterns between pine, larch and spruce dominated habitats in the pristine taiga (Cajander 1905, 1909) and the transition from woodlands and to grasslands in the tropics (Walter 1964), was developed to a rigorous, formal hypothesis by Tilman (1982, 1988). Since competition is likely to lead to exclusion of species from the system (Cajander 1909, Gause 1934), the importance of competition is also connected to issues of local (alpha) species richness (Grime 1973, 1979, Al-Mufti et al. 1977, Connell 1978, Grytnes 2000, Rajaniemi 2003).

The problem has been attacked in numerous field and greenhouse experiments and in reviews (meta-analyses) of their results. Some studies report a positive relationship between primary productivity and competition intensity (Wilson and Keddy 1986*a*, Campbell and Grime 1992, Turkington et al. 1993, Bonser and Reader 1995, Gaudet and Keddy 1995, Kadmon 1995, Sammul et al. 2000, Callaway et al. 2002), while in other studies, no such relationship has been detected (Welden et al. 1988, DiTomasso and Aarssen 1991, Wilson and Shay 1990, Wilson and Tilman 1991*ab*, 1993, Gurevitch et al. 1992, Cahill 1999), or the intensity of competition has even been found to correlate *negatively* with primary productivity (Goldberg et al. 1999). Goldberg and Novoplansky (1997) proposed that the primary reason for the discrepancy lies

in the contrast between the impacts of constantly low and pulsating resource levels. Goldberg and Barton (1992), in turn, emphasised the contrast of experimentally created and natural productivity gradients and suggested that co-variation between productivity and some other factors, such as grazing pressure (Oksanen et al. 1981), fire (Barton 1991), or some other form of physical disturbance (Wilson and Keddy 1986*ab*) accounts for the positive correlation between competition intensity and primary productivity along natural productivity gradients.

There also is some evidence that increasing competition intensity with increasing productivity is a result of changing species composition (Peltzer et al. 1998). Moreover, it has been shown that local species richness is in good positive correlation with regional species pool at low level of productivity, but is independent of species pool at higher productivites (Huston 1999, Pärtel et al. 2000), where competitive pressure is expected to be higher. Broadly, these studies have led to conclusion that the relative importance of species pool and local interactions in determining local species richness is changing along the gradient of productivity (Pärtel et al. 2000). Already Cajander (1909) proposed that large species pool should reduce the likelihood of competitive exclusion, because it is likely to contain many species with subtle niche differences, sufficient to allow for competitive coexistence. However, this argument could just as well be reversed. The larger the species pool, the larger the expected number of species with similar niches and the more there is room for competitive exclusion to operate. As compared to the voluminous literature concerning the relationship between competition intensity and productivity, the relationship between competition intensity and species richness has obtained little attention (but see Gurevitch and Unnasch 1989).

In the present paper, we report results of a competition experiment focusing on the response of a medium sized rosette forb, the North European goldenrod (*Solidago virgaurea)* on removal of competitors along two different kinds of productivity gradients found in northern Europe. One of these lies in Estonian limestone areas, where the limiting resource is water. The other lies in Finnmark, northernmost Norway, where rocks are primarily silicaceous and productivity is controlled by several factors (temperature, duration of growing season, disturbance, nutrient availability, moisture). While their productivities overlap, the species pools of the two areas are very different, both qualitatively and quantitatively at high latitudes, limestone areas harbor for historical reasons a much larger species pool than areas underlain by acidic, silicaceous rocks, see Grubb [1987], Dynesius and Jansson [2000], Pärtel [2002]). Any pattern where communities from the two areas behave consistently is indicative of the impact of productivity, while direct impacts of physical factors or species pool should be reflected as differences between the relationships found in the two areas. Moreover, the North Norwegian study area has been since 1977 focus for intensive studies on herbivore-plant and carnivore-herbivore interactions (summarised by Oksanen et al. 1997 and Oksanen and Oksanen 2000). In the

herbivory issue, our study can thus rely on a large base of published data. We also have conducted a parallel study focusing on a grass *Anthoxanthum odoratum*, which has wide habitat amplitude in both areas (Sammul et al. 2000). We can thus check the robustness of the results reported below by comparing two independent studies.

STUDY AREAS

Habitats and productivity patterns

The removal experiment was conducted with the perennial herb *Solidago virgaurea* (further on referred to as *Solidago*) in two geographically distant (1400 km) regions: coastal Estonia and Finnmark, northernmost Norway during 1997–1998. In Estonia, the experiment was conducted on the western coast in Laelatu wooded meadow and its neighbouring meadow communities (58°35'N, 23°34'E, altitudes < 25 m.a.s.l.), within the Laelatu-Puhtu-Nehatu Nature Reserve and on the adjacent Sillukse alvar (see Table 1). The area belongs to the hemiboreal zone (Ahti et al. 1968) representing the transition between temperate deciduous forests and the taiga. The mean temperature for July is +17.0 °C and for January –5.0 °C; the mean annual precipitation is 600 mm. The landscape is rather flat but heterogeneous, being a mosaic of numerous small forests, scrublands, meadows, fields and urban areas. The bedrock is Silurian limestone, which creates neutral or basic site conditions.

The productivity of the area is strongly influenced by the spring and early summer droughts, typical for the shores of the Baltic Sea. The severity of this periodic drought depends on soil conditions. Deep soils retain moisture from the rains and snow of the winter, whereas the drought gets severe in habitats with shallow soils. In this land-lift area, which was submerged after the deglaciation, soil was washed from uplands to depressions. Hence, the elevated parts of the landscape are characterised by leached limestone flats with little or no soil, and occupied by barren calcareous meadows, referred to as alvars (Pärtel et al. 1999). Productive bottomlands are today occupied by mixed forests, unless they have been converted to cropfields. In some areas, these habitats still support wooded meadows, which are products of the traditional land use and are today maintained by simulating the old land use practices (selective logging and haymaking, see Kukk and Kull 1997).

In northern Norway, the experiment was conducted at a Joatkanjávri, Alta, Finnmark (69°46'N, 23°58'E); altitudes 380–600 m above sea level. The lower parts of the area belong to the hemiarctic zone, where tundra prevails but woodland patches occur in topographically favourable sites. Above the 450 m contour, the landscape is arctic-alpine: trees are absent and the tallest woody

plants are knee-high willow shrubs. The area has a continental and relatively arid climate, annual precipitation being only 350 mm, mean July temperature +10°C, and mean February temperature about −12°C (Oksanen and Virtanen 1995). Rocks are acidic, but nutrient-rich, non-calcareous schists abound along the thrust line of the Scandinavian mountain chain. Thus, primary productivity is influenced by several factors (e.g. altitude, exposition, edaphic moisture, bedrock). Highest productivities occur on the lower parts of the thrust line, where all local factors are maximally favourable. Lowest productivities are found on summits and in late snow-beds. In both areas, there are many communities, where the target species, *Solidago virgaurea,* is reasonably abundant, and in both areas, these habitats cover large pieces of local productivity gradients. The characteristics of these target habitats are summarised in Table 1.

Grazing and other disturbance in the study areas

Since correlation between disturbance and productivity, including productivity-driven changes in trophic dynamics, is one of the proposed reasons for statistical relations between primary productivity and competition intensity (Oksanen, L1990, Goldberg and Barton 1992), it is essential to summarise the evidence for patterns in grazing and other disturbance in the study areas. For the Estonian area, we do not have data on densities or dynamics of native grazers or on their impacts on the vegetation. However, the treeless alvars were created by intense grazing by domesticated animals and require grazing or mowing for their persistence (Pettersson 1958, Pärtel et al. 1999). The wooded meadows, in turn, were utilised for production of winter fodder. They were left untouched in early summer, allowing the biomass to accumulate. In mid-summer, they were mown and sometimes grazed thereafter (see also Kukk and Kull 1997). Currently, mowing is mostly practiced as a means of habitat preservation. During the experiment, the study sites were not mown.

In the arctic-alpine habitats of Fennoscandia, the main grazers are the migratory reindeer and microtine rodents (Wielgolaski 1975). Our study area lies in the migration zone, where reindeer are mainly present before the snowmelt (in April-May) and after the growing season (in September-November). The area harbors a diverse guild of microtine rodents, which had relatively high densities during the study period (Ekerholm et al. 2001). The three other unmanaged herbivorous endotherms — the mountain hare (*Lepus timidus*), the willow grouse (*Lagopus lagopus*) and the (rock) ptarmigan (*L. mutus*) — fluctuate in numbers, following the vole cycles.

With respect to predator-vole and vole-vegetation dynamics, the study area harbors two entirely different kinds of habitats. The most productive woodlands, scrublands and tall-herb meadows are characterised by constant presence and periodically high numbers of predators (primarily small mustelids,

see Oksanen and Oksanen 1992, Oksanen et al. 1992*b*, 1997, 1999). Due to the intense predation pressure, densities of microtine rodents are roughly on the same level as in essentially less productive shrubby dwarf birch tundra and snow bed habitats (Oksanen et al. 1999, Moen and Oksanen 1998). In the lush and herb rich habitats, these densities do not suffice to exert any impact on the vegetation. The survival of herbaceous plants is practically 100% even in vole outbreak years (Oksanen and Ericson 1987), and exclusion of grazing mammals has no detectable impact on the vegetation (Moen and Oksanen 1998), including competition between plants (Olofsson et al. 2002).

A totally different situation prevails in less productive tundra habitats. Here predators are practically absent. Patterns in density fluctuations of rodents indicate resource limitation (Turchin et al. 2000, Ekerholm et al. 2001) and spatial patterns in densities of microtine rodents match spatial patterns in productivity (Oksanen et al. 1999). Rodent impact on vegetation is severe in vole years (Moen et al. 1993), especially for the relatively preferred *Solidago*, which then suffers high rates of shoot mortality (Oksanen and Ericson 1987). In these habitats, exclusion of herbivorous mammals has strong impact on the vegetation (Oksanen 1988, Oksanen and Moen 1994, Moen and Oksanen 1998, see also Virtanen1998, 2000, Virtanen et al. 1997) and on the intensity of plant-plant competition.

MATERIAL AND METHODS

Experimental design

Sixteen different herbaceous communities (8 in each country) of different productivity and similar light conditions were chosen. In Estonia, 16–30 individual plants (genets) of *Solidago* (depending on the number of plants found in the community in early spring 1997) and in Norway 20 plants were marked in each community and followed through two growing seasons. Initially, all genets consisted of a single ramet (sensu Harper 1977), were sterile, and had 2 to 3 leaves. In the course of the experiment most genets developed several ramets. The plants were randomly divided into two groups: removal of neighbours (treatment) and control. The number of plants in both groups was equal.

In order to reduce competition, the aboveground parts of all neighbouring plants were removed by hand from an area with a radius of 15 cm around the treatment *Solidago* plants. Re-growth of neighbouring plants was controlled by hand-weeding several times during the growing season. Although the direct manipulation was restricted to shoots, recurrent weeding influenced the overall vitality of the neighbours as indicated by the sharp decrease in the amount of

regrowth already after second weeding. Thus, also competition for soil resources was reduced. Removal of the shoots of the neighbours around the already existing plants was preferred to a transplant experiment and trenching was not used, since we wanted to retain the other structural aspects of the community as well as to keep the soil intact. The latter is especially important in the tundra, where disturbance by frost or by mobile surface water is often severe and any disruption of the soil surface amplifies the impact of these factors.

Altogether 80 control and 80 treatment plants were marked in each area (total 320 plants). Marking of the plants and the first removal of neighbours were performed in May 1997 in Estonia and in June 1997 in Norway. In both countries, this is springtime. The experiment was finished in early autumn 1998 in both countries, i.e. in late August in Norway and in mid-September in Estonia. The biomass collected from the manipulated plots at the beginning of the experiment was separated into two fractions: living biomass and litter. Woody stems were included in the litter fraction, because we wanted to obtain biomass estimates that reflect productivity and leaf area index. To obtain a more reliable index of primary productivity, the aboveground plant parts of the field layer were collected at the time of maximum living biomass (in July in Estonia and in August in Norway) in 1997 from three randomly located samples of 10*30 cm per community and separated in the fractions as described above. Due to high variation in the collected samples of biomass, the latter sampling procedure was repeated in all Estonian communities in 1998. All samples were dried at 78 °C for 48 h and weighed to an accuracy of 0.1 g. The procedure was also repeated for control plots at the end of the experiment in 1998.

In each plot the number of shoots and the number of species were counted in an area with a radius of 7 cm around the experimental plants at the beginning of the experiment. Counting was repeated in midsummer and in early autumn in control plots in 1997. From these vegetation analyses, the average number of species per plot was extracted using the midsummer censuses (further referred to as the average number of species), and the cumulative number of species per community was calculated using all vegetation analyses from one community.

The numbers of leaves and ramets of *Solidago* were counted 3–4 times a year. At the end of both growing seasons the aboveground parts of *Solidago* were collected from all plots. To estimate the biomass of the belowground parts, a clod of soil with a radius of 15 cm and with an approximate thickness of 10–15 cm around each experimental plant was dug up at the end of the experiment in 1998. The depth of excavation depended on local soil conditions and was always larger than the depth of the humus layer. The belowground parts of the experimental plants were cleaned from soil using running water and separated into rhizomes and roots. All plant parts were dried at 78°C for 48 h and weighed to an accuracy of 0.01 g.

Data analysis

As a measure of the intensity of competition, we used the *CRCI* index, which is derived from the classical *RCI* index by correcting for its built-in mathematical flaws. First, we divided the difference between the total biomass of treatment and control plants by the total biomass of the plant, which had performed better, to create an unbiased index with symmetric behaviour at positive and negative index values, as proposed by Markham and Chanway (1996). Second, we arc sin transformed the index to linearize it (see Oksanen et al. 2003). The formula for *CRCI* thus obtained is as follows:

$$CRCI = arc\ sin\ (\ (X_r - X_c)\ /\ (\ max\ X_r, X_c)\ )\qquad \text{Eq. 1,}$$

where X_r is the total biomass of plants whose competitors have been removed and X_c is the total biomass of the controls. The biomass used in the calculation is the average biomass of all plants belonging to one of the treatments in a single community. *CRCI* values derived from various kinds of pair-wise comparisons between treatment and control plants, are presented by Oksanen et al. (2003). To determine the effects of treatment on the aboveground, belowground and total biomasses of *Solidago*, the nested subset ANOVA was used, with the 16 communities nested in 2 geographical regions (Estonia and Norway). All factors were treated as fixed factors. The data were analysed using the program Statistica 5.0 (StatSoft 1995).

The first step in our test was to ask whether competition has a statistically significant impact on the biomass of *Solidago* in a given community (post-hoc Tukey HSD test). We then proceeded by asking whether the effect of the treatment could be detected for the material as a whole and whether there was evidence for a regional difference in its magnitude. Thereafter, we tested whether the intensity of competition (*CRCI)* varied as a function of primary productivity, and whether local species richness was related to *CRCI*. For this we applied standard regression technique, with community-specific estimates of productivity, *CRCI* and numbers of species as input variables. If a statistically significant relationship was detected, we proceeded by computing the residuals for data points from the two subareas to find out whether there were differences between Estonia and northernmost Norway in the relationships between *CRCI* and productivity or species richness. If the distribution of the residuals for the two areas was non-random, separate regressions were computed for the two subareas. In the analyses of the impact of productivity on competition intensity, we also tested whether the y-intercept of the regression was significantly different from zero.

RESULTS

The effect of the treatment and community biomass on the size of *Solidago*

The majority of the within-community tests of the effect of the treatment (Tukey HSD test) failed to reveal significant differences in the biomasses between the control plants and the manipulated plants. The only statistically significant differences were found in Estonian communities with medium productivity, where the total biomass of the manipulated plants was larger than the total biomass of the control plants (Laelatu wooded meadow III: $p < 0.036$, Puhtu seashore meadow III: $p < 0.013$). This was due to difference in aboveground biomass between treatments and controls ($p < 0.022$ and $p < 0.0001$ respectively). None of such differences were significant for belowground biomass.

The main effect of the community was significant for all biomass measures of plants, indicating that there were considerable differences in plant size between the communities (Table 2). The same applies to the main effect of the geographic location (Table 2, Figure 1), as *Solidago* plants are considerably bigger in Estonia than in Norway with regard of both above- and belowground biomass, in spite of differences between the treatments. A significant positive effect of the removal treatment was detected on the aboveground biomass and on the total biomass of *Solidago*. Similar effect of the treatment on the belowground biomass of *Solidago* was only marginally significant (Table 2). The interaction of treatment effect with the effect of the geographic location was also significant for all the biomasses of plants, so that in Estonia the manipulated plants were larger than the control plants, while in Norway this difference was not significant (Fig. 1). Moreover, even the Estonian plants growing in competitive environment were bigger thatn the Norwegian plants growing without competition ($p<0.018$ for aboveground biomass and $p < 0.0001$ for belowground and total biomass). The interaction between the effects of the treatment and community type was significant only for the aboveground biomass of *Solidago* plants.

Both aboveground and belowground biomass of the manipulated plants were marginally positively correlated with community living biomass ($0.053 < p < 0.064$). These relationships resulted in statistically significant increase of total biomass of manipulated *Solidago* plants with increasing community productivity (Table 3). No relationship between any of the biomasses and productivity of the community was detected for control plants. When different geographical regions were analysed separately, neither the size of the manipulated plants nor the size of the control plants changed along the productivity gradient.

Relationships between CRCI and community productivity

CRCI was positively correlated with community living biomass when Estonian and Norwegian data were pooled (Table 4, Fig. 2). The 95% confidence bands showed that in the productivity range 0...170g m^{-2} the *CRCI* did not differ significantly from 0, but starting from productivity over 170g m^{-2} *CRCI* became significantly positive. The estimated y-intercept of the regression line was negative (y =–0.25) but statistically not significant (Table 4). The means (± standard error) of the residuals of this regression were 0.7±0.08 for the Estonian data, and for Norwegian data –0.7±0.07 and they were different from 0 and from each other at $p<0.001$. Thus, these results suggest that other regional differences beside those caused by differences in productivity contribute to this regression. The same regression was marginally significant for Estonian data ($p<0.1$) with virtually equal slope of the regression but intercept slightly closer to 0. No relationship between plant living biomass of the community and *CRCI* was observed for Norwegian data (Table 4).

We detected significant negative relationship between *CRCI* and amount of litter for Norway and this relationship was strong enough to cause marginally significant decrease of *CRCI* with increasing total biomass (incl. litter) of the ground layer in Norway (Table 4).

Results derived from pair-wise comparisons between treatment and control plants yield practically identical results, so do results obtained using the *lnRR* index (Oksanen et al. 2003).

Relationships between CRCI and community species richness

We did not find any correlation between *CRCI* and community species richness for the pooled data. However, there was a negative correlation between both average and cumulative species richness and *CRCI* in Estonia (Fig. 3, Table 5). No significant relationship was found between either measure of species richness and *CRCI* in Norway.

Relationships between species richness and community productivity

We found marginally significant increase of both average and cumulative species richness with increasing living biomass of the community in Norway ($p<0.08$, Table 6). In Estonia, on the other hand, the negative effect of litter on species richness was marginally significant ($p<0.08$). Moreover, there was even a statistically significant negative relationship between cumulative number of species and amount of plant litter in the case of pooled data (Table 6).

DISCUSSION

Competition, facilitation, and primary productivity

The relationship between competition intensity and community productivity, established in this study (Figure 2) is very similar to that found in our previous experiment with *Anthoxanthum odoratum* (Sammul et al. 2000) and in the set of experiments of Callaway et al. (2002), indicating that competition intensity increases with increasing community productivity (e.g. Grime 1973, Berendse 1983, Wilson and Keddy 1986*ab*, Campbell and Grime 1992, Kadmon 1995). The maximum value of the y-intercept, consistent with the confidence limits of our regression line, is only +0.08, indicating that competitive interactions disappear when primary productivity approaches zero, assuming that the relationship is linear. If the negative y-intercept is also considered, then our results indicate plant-plant relationship change from competitive to mutualistic along the gradients of decreasing community productivity, as proposed by Callaghan and Emanuelsson (1985).

We regard it as unlikely that a shift from the prevalence of aboveground competition to belowground competition alone (Tilman 1988, Belcher et al. 1995) would suffice to account for these results. Even though our manipulation of belowground competition was indirect, recurrent removal of shoots reduces the overall vitality of the neighbouring plants. It seems reasonable to assume that the correlation between the growth rate of roots and primary productivity is positive, because the factors reducing primary productivity tend to have a negative impact on all growth processes. Low annual rates of root growth are especially probable in snow-bed communities, which differ from more productive communities primarily in having a shorter and cooler growing season. We can thus expect that the impact of our treatment on belowground competition in less productive communities was either stronger than or equal to the impact in more productive communities.

The role of grazing for the relationship between productivity and plant-plant competition

For our study areas, we have direct evidence corroborating the conjecture of Goldberg and Barton (1992) that the relationship between primary productivity and intensity of plant-plant competition is created by co-variance between primary productivity and the intensity of natural herbivory. In extreme high alpine barrens, where grazing mammals are absent due to the scantiness of forage (Oksanen et al. 1996), the removal of the dominating *Ranunculus glacialis* has a big positive impact on the establishment and growth of *Oxyria digyna*, indicating intense pre-emptive competition for the few microsites,

where plant growth is still possible (Olofsson et al. 1999). Moreover, Olofsson et al. (2002) conducted two parallel competition experiments in one of the unproductive habitats, where our study indicated that competition intensity was close to zero. One experiment, conducted on open plots yielded results consistent with ours. Another experiment, conducted in decade-old mammal exclosures, yielded totally different results. Competition was found to be as intense as it was in maximally productive tall herb meadows. Moreover, the productive habitats are intensely utilised by predators (Oksanen et al. 1992*a*, 1997, 1999) and their removal has strong, positive impact on the densities of grazing mammals (Ekerholm et al. 2003). In the habitat gradients of northernmost Norway, low intensity of competition in unproductive habitats thus appears to be a consequence of periodically intense herbivory. On the alvars of the Baltic coasts, the role of grazing is even more obvious. Alvars are products of long-lasting intense grazing (Pärtel et al. 1999*a*) and do not even persist without grazing or mowing (Pettersson 1958, Rosén 1982, Pärtel et al. 1999*b*) but are overgrown by competitively superior *Juniperus communis* or some other shrubs or trees.

Whether herbivory could account for the facilitative plant-plat relationships, documented in several arctic-alpine systems (Carlsson and Callaghan 1991, Callaway et al. 2002) and indicated by our results, too, is a more complicated issue. Relatively palatable herbaceous plants such as *Solidago virgaurea* and *Carex bigelowii* (Aleksandrova et al. 1964) suffer substantial levels of mortality in years of high rodent numbers (Oksanen and Ericson 1987) and are favoured by the exclusion of herbivorous mammals (Virtanen 1998). Close association with less palatable species might offer protection against herbivory. On the other hand, most herbivory in arctic-alpine habitats occurs in winter (Hambäck and Ekerholm 1997), while summer herbivory is so sporadic that the herbaceous habit can be regarded as a successful defensive strategy (Hambäck 1998). Even in the experiments of Olofsson et al. (2002), the intensification of competition in herbivore exclosures was obviously a consequence of gradual build up of plant biomass. No dramatic herbivory effects could be seen on open plots under summer conditions. It is thus possible that the facilitation observed in arctic-alpine barrens is genuine and derives from the ameliorating effect of increased shoot density on the physical environment (e.g. reduced wind velocity and thus increased near-ground temperatures on sunny days) in the very same way as plant cover on alvar grasslands ameliorates edaphic moisture conditions during hot and dry midsummer.

New evidence has only strengthened the case of Goldberg and Barton (1992). New results supportive to the idea that competition intensity is low in unproductive environments (Kadmon and Shmida 1999, Kadmon et al. 1995, Virtanen 1998, Moen and Oksanen 1998, Sammul et al. 2000, Callaway and al. 2002) are obtained in studies, which are primarily Eurasian and have been conducted along such productivity gradients, where the unproductive habitats are natural or have been created by long-lasting intense grazing (notice the

enormous abundance of such habitats in Eurasia, see Walter 1968, Gimingham 1972). Conversely, even the new studies, where competition intensity between plants was found to be independent of primary productivity (Bonser and Reader 1995, Cahill 1999, 2002), have mostly been conducted along small-scale local (often artficial) productivity gradients in North America, commonly on successional old-fields. Such studies also constitute the bulk of the data base of Goldberg et al. (1999) and this may contribute to their unexpected finding of decreasing competition intensity with increasing productivity. As the integrated international project of Callaway et al. (2002) did not reveal any differences between New World and Old World systems, we regard it as likely that the apparent cross-Atlantic difference rather stems from cultural differences in the selection of study systems rather than any genuine cross-Atlantic difference in community dynamics.

If differences in trophic dynamics within the endotherm branches of terrestrial grazing chains account for spatial patterns in the intensity of plant-plant competition (Oksanen et al. 1981, Oksanen, L. 1990, Oksanen and Oksanen 2000), then spatial scale and distribution of communities should be important indeed, because the activity areas of grazing mammals, folivorous birds and their predators are fairly large. Moreover, populations of predators are likely to have source-sink dynamics, bringing predators even to unproductive habitats in those landscapes, where productive habitats abound (Holt 1984, 1985, Oksanen, T. 1990). Moreover, predators can be subsidised by resources produced in more productive systems (Polis and Strong 1996), and transient predators, passing through unproductive habitats, can be expected to be engaged in opportunistic predation if a prey is encountered (Oksanen et al. 1992*ab*). All these mechanisms should contribute to 'spillover predation' in unproductive habitats, embedded in a productive landscape. This should erase all between-habitat differences between local intensities of herbivory in landscapes, where productive habitats abound. If the underlying cause for the pattern lies in productivity-driven changes in grazing (Oksanen et al. 1981, Oksanen, L. 1990, Oksanen and Oksanen 2000), it is thus entirely natural that the pattern is seen in large-scale gradients from moist and warm areas to arctic, alpine and arid barrens but not in gradients provided by small-scale experimental systems or by old fields, embedded in productive humid-temperate landscapes.

Competition and local species diversity

It is often proposed that undisturbed competition for a single limiting resource, such as light or space, results in low species diversity and that high productivity increases the likelihood of a strong limitation by a single resource (Grime 1973, Connell 1978, Tilman 1988, Huston and DeAngelis 1994). Indeed, the evidence analysed so far and our current results suggests that local species richness

declines along the gradients of increasing productivity if and only if the intensity of competition increases (Goldberg and Estabrook 1998). In studies reporting decreasing species richness with increasing productivity, increasing competition for a single resource is often proposed as an explanation for the pattern (e.g. Grace and Pugesek 1997, Grytnes 2000, see also review by Rajaniemi 2003). However experiments concerning the relationship between competition and species diversity have been seldom conducted and the two issues are rarely explicitly dealt with within the same study (but see Grime 1973, Goldberg and Miller 1990, Goldberg and Estabrook 1998, Gurevitch and Unnasch 1989, Lepš 1999).

Our study contributes to this still small body of evidence by suggesting that the relationship between competition intensity and species diversity is strong in systems with a large species pool, such as the Estonian grasslands and meadows on limestone bedrock. The same pattern is found even in lime influenced habitats of northernmost Fennoscandia. In Kalliola's (1939) material, representing Finnish tundra areas adjacent to Finnmark, the maximally productive willow thickets harbor only 10–20 (mean 13.9) vascular species and 3–6 (mean 4.6) cryptogam species per $4m^2$ The less productive *Dryas* heaths on lime-rich soils harbor 23–30 vascular species (mean 26.1) and 11–26 cryptogam species (mean 16.3) per $4m^2$ Within the Scandinavian mountain chain proper, where lime-rich habitats are more common, their species richness is even higher (Virtanen and Eurola 1997). Thus, the crucial factor seems to be the bedrock, not the latitudinal position of the system (see also Pärtel 2002).

In the North Norwegian habitats included in our study, species richness is consistently on the same low level as found in the most productive Estonian communities with highest intensity of competition. It would be tempting to interpret this as evidence for the conjecture that in species poor areas, interspecific niche differences between potentially coexisting plants are sufficient to allow for their competitive coexistence. Recall, however, that the soft shales and the impact of running water, which account for the relatively high productivity of the most luxuriant study sites in northernmost Norway, probably influence pH and thus the pool of the species capable of growing in the site. It is thus possible that the negative relationship of local species diversity to productivity and competition intensity exists generally even in northern Fennoscandia, but the trend is masked in our material, because the decreasing intensity of competition happens to be associated with decreasing pH and hence with the decreasing size of the species pool (Grubb 1987, Pärtel 2002). In the case of studied Estonian communities, however, the species pools of more productive and less productive communities do not differ, since they are all calcareous grasslands within relatively small geographical range and share most of the species. Therefore, the number of species capable for immigration and successful growth is quite high and decreasing intensity of competitive interactions allows for more species to establish and persist resulting in high number of coexisting species.

While species pool indeed sets the upper limit for the number of coexisting species (Zobel 1997, Herben 2000, Gaston 2000), local processes determine the number of species actually coexisting in a given community. Our results concerning the role of competition for local species richness in lime-influenced communities are concordant with the very rapid decrease in species richness in abandoned wooded meadows (Kukk and Kull 1997) and on those alvars, which are no longer grazed (Pettersson 1958, Rosén 1982). Moreover, local processes, such as cessation of grazing, may influence species pool as exemplified by the currently threatened status of several alvar plants and decreasing abundance of red-listed arctic-alpine plants on mountains from where reindeer had been excluded (Olofsson and Oksanen unpublished data). For us, it is easier to understand the origin of both large-scale patterns (e.g. high species diversity on neutral and nutrient-rich soils in Eurasia and the reverse situation in Australia and South Africa) as well as local patterns, if we assume that local processes are crucial for their development and that the role of long time spans and climatic stability (Zobel 1992, Tilman 1997, Grace 1999, Smith and Knapp 2001) is that under these conditions, evolution driven by local processes can successively enrich the flora. If, however, undisturbed competition for a single resource prevails, competitive exclusion will rule, and no amount of time and stability will lead to increased species richness, neither locally nor regionally

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Table 1. Characteristics of the studied communities.

Community	Location	Plant living biomass (g/m^2)	Plant litter (g/m^2)	Cumulative number of species	Elevation above sea level (m)	Main dominant plant species
Sillukse alvar	Estonia	113	429	32	<25	*Festuca rubra, F ovina, Helictotrichon pratense*
Laelatu alvar	Estonia	144	254	42	<25	*Sesleria caerulea, Carex tomentosa, Festuca pratensis*
Laelatu wooded meadow I	Estonia	212	347	24	<25	*Brachypodium pinnatum, Poa angustifolia, Convallaria majalis*
Laelatu wooded meadow II	Estonia	177	385	31	<25	*Brachypodium pinnatum, Carex tomentosa, Convallaria majalis*
Laelatu wooded meadow III	Estonia	159	367	26	<25	*Brachypodium pinnatum, Carex tomentosa, Convallaria majalis*
Puhtu meadow I	Estonia	263	463	18	<25	*Brachypodium pinnatum, Carex tomentosa*
Puhtu meadow II	Estonia	359	387	32	<25	*Helictotrichon pratense, Brachypodium pinnatum*
Puhtu meadow III	Estonia	244	354	25	<25	*Brachypodium pinnatum, Carex tomentosa, Sesleria caerulea, Helictotrichon pubescens, H. pratense*
Snow-bed I	Norway	95	300	13	580	*Salix herbacea, Festuca ovina*
Snow-bed II	Norway	49	219	9	540	*Salix herbacea, Festuca ovina, Vaccinium myrtillus*
Heath	Norway	160	942	10	510	*Empetrum nigrum, Vaccinium myrtillus, Arctostaphylos uva-ursi*
Clear-cut area I	Norway	168	525	18	440	*Cornus suecica, Trollius europaeus*
Clear-cut area II	Norway	141	678	10	420	*Cornus suecica, Vaccinium myrtillus*
Clear-cut area III	Norway	231	405	21	460	*Cornus suecica, Vaccinium myrtillus, Gymnocarpium dryopteris*
Riverside	Norway	107	846	12	389	*Vaccinium myrtillus, Empetrum nigrum*
Riverbank meadow	Norway	191	374	31	388	*Trollius europaeus, Carex vaginata, Vacciniummyrtillus*

Table 2. Results of the nested subset ANOVA. Statistically significant differences ($p<0.05$) are in bold script.

Dependent variable	Source of variation	df Effect	MS Effect	df Error	MS Error	F	P
Aboveground biomass	Location (country)	1	69.4	282	0.80	86	**<0.0001**
	Treatment	1	22.1	282	0.80	27	**<0.0001**
	Community	14	3.6	282	0.80	4.5	**<0.0001**
	Location*Treatment	1	16.3	282	0.80	20	**<0.0001**
	Community*Treatment	14	1.5	282	0.80	1.8	**0.036**
Belowground biomass	Location (country)	1	85.8	282	0.82	104	**<0.0001**
	Treatment	1	2.6	282	0.82	3.2	0.076
	Community	14	5.0	282	0.82	6.1	**<0.0001**
	Location*Treatment	1	3.8	282	0.82	4.6	**0.033**
	Community*Treatment	14	0.8	282	0.82	0.92	0.534
Total biomass	Location (country)	1	310	282	2.47	125	**<0.0001**
	Treatment	1	40	282	2.47	16	**<0.0001**
	Community	14	16	282	2.47	6.6	**<0.0001**
	Location*Treatment	1	36	282	2.47	14	**0.0002**
	Community*Treatment	14	3.9	282	2.47	1.6	0.081

Table 3. Relationships of aboveground, belowground and total biomasses of *Solidago* to community living biomass (independent variable). The pooled data of Estonian and Norwegian plants are included in analysis. Statistically significant p-values ($p<0.05$) are in bold script.

Dependent variable	Treatment	Regression	P	R^2
Aboveground biomass	Manipulation	$y = 0.006\ x - 0.028$	0.054	0.24
	Control	$y = 0.001\ x + 0.432$	0.702	0.01
Belowground biomass	Manipulation	$y = 0.006\ x + 0.416$	0.063	0.23
	Control	$y = 0.002\ x + 0.841$	0.379	0.06
Total biomass	Manipulation	$y = 0.012\ x + 0.388$	**0.049**	0.25
	Control	$y = 0.003\ x + 1.273$	0.491	0.03

Table 4. Relationships between community aboveground biomass (independent variable) and *CRCI* (dependent variable). Statistically significant p-values ($p < 0.05$) are in bold script.

Independent variable	Location	Regression	R^2	p-value of slope	p-value of intercept
Living biomass	Estonia	y=–0.15+0.0023x	0.393	0.096	0.601
	Norway	y=–0.07+0.0005x	0.024	0.712	0.708
	Estonia + Norway	y=–0.25+0.0023x	0.371	**0.012**	0.128
Litter	Estonia	y=–0.28+0.0016x	0.116	0.409	0.698
	Norway	y= 0.25–0.0005x	0.581	**0.027**	**0.042**
	Estonia + Norway	y= 0.46–0.0004x	0.213	0.072	**0.016**
Total biomass	Estonia	y=–0.62+0.0016x	0.38	0.104	0.261
	Norway	y= 0.27–0.0004x	0.473	0.059	0.077
	Estonia + Norway	y= 0.36–0.0003x	0.051	0.399	0.154

Table 5. Relationships between the corrected coefficient of relative competition intensity (*CRCI*) (independent variable x) and community species richness (dependent variable y: average number of species per 155 cm^2 or cumulative number of species per community). Statistically significant p-values ($p<0.05$) are in bold script.

Location	Average number of species			Cumulative number of species		
	Regression	P	R^2	Regression	P	R^2
Estonia	y=12.4–8.32x	**0.046**	0.512	y=34.6–17.6x	**0.045**	0.51
Norway	y=7.0+3.50x	0.58	0.053	y=15.6+14.6x	0.44	0.10
Estonia + Norway	y=8.4–0.68x	0.82	0.004	y=20.9+7.86x	0.4	0.05

Table 6. Relationships between community aboveground biomass (independent variable x) and average or cumulative number of species (dependent variable y). Statistically significant p-values ($p < 0.05$) are in bold script.

Independent variable	Location	Average number of species			Cumulative number of species		
		Regression	P	R^2	Regression	P	R^2
Living biomass	Estonia	y=11.9 –0.01x	0.56	0.06	y=35.8–0.03x	0.38	0.13
	Norway	y=2.9+0.028x	0.08	0.42	y=2.92+0.088x	0.07	0.46
	Estonia + Norway	y=6.4+0.01x	0.35	0.06	y=13.5+0.049x	0.16	0.26
Litter	Estonia	y=23.6–0.037x	0.07	0.45	y=57.0–0.075x	0.08	0.41
	Norway	y=8.4–0.003x	0.48	0.08	y=20.7–0.01x	0.41	0.12
	Estonia + Norway	y=11.3–0.007x	0.11	0.17	y=33.6–0.025x	**0.04**	0.26
Total biomass	Estonia	y=19.4–0.017x	0.16	0.30	y=52.0–0.04x	0.11	0.37
	Norway	y=7.8–0.001x	0.74	0.02	y=18.8–0.005x	0.67	0.03
	Estonia + Norway	y=11.3–0.005x	0.24	0.10	y=32.9–0.02x	0.17	0.13

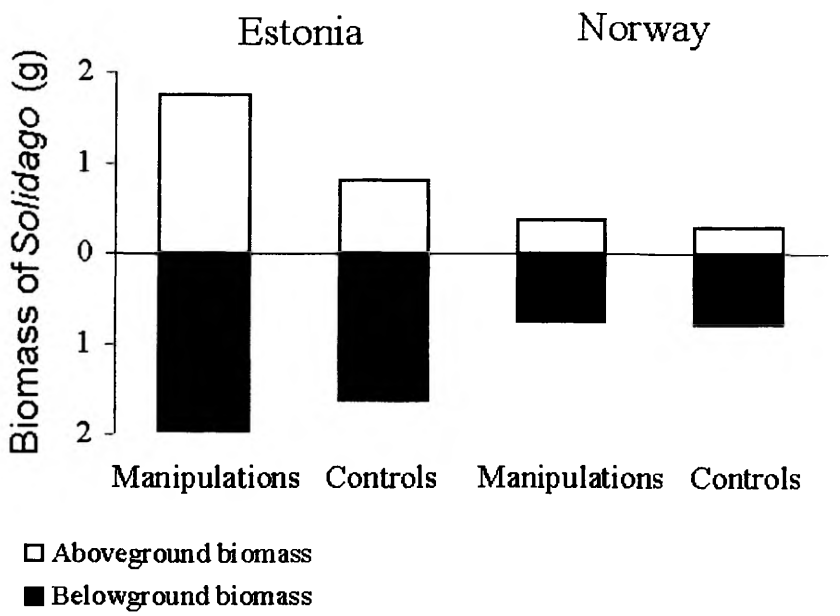

Fig. 1. Biomasses of manipulated and control *Solidago* plants in Estonia and in Norway at the end of experiment.

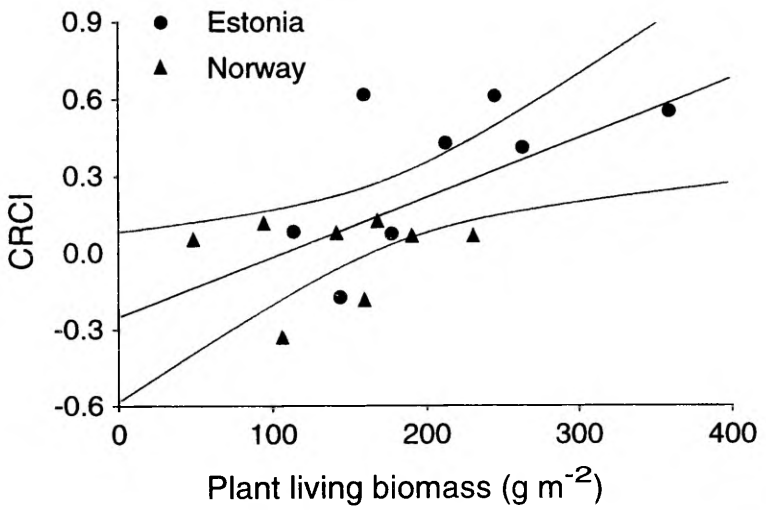

Fig. 2. Relationships between average community living biomass and competition intensity (*CRCI*). Regression is presented for the pooled Estonian and Norwegian data and it is statistically significant at $p<0.013$; for the results of regression see Table 4.

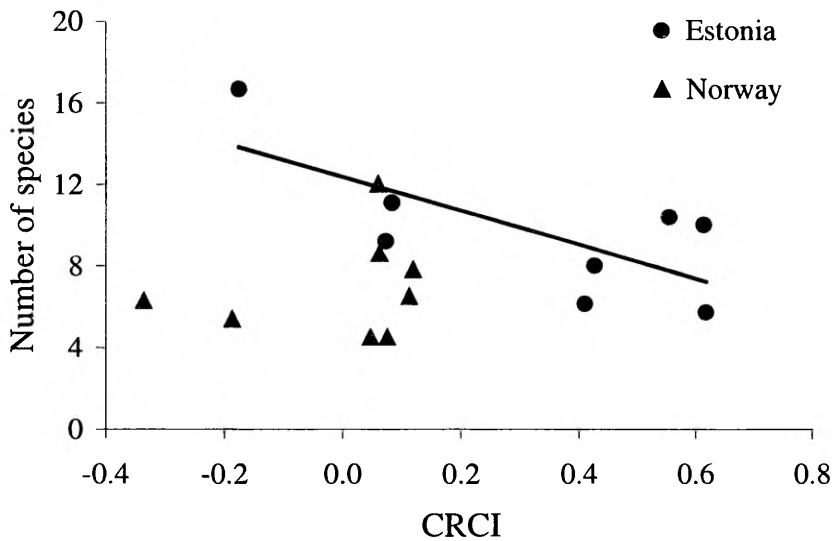

Fig. 3. Relationships between average community species richness (number of species per 155 cm^2 in the midsummer) and competition intensity (*CRCI*). Regression (significant at $p<0.05$) is presented only for the Estonian data; for the results of regression see Table 5.

III

OLE MAALÄHEDANE

Maa on Tüng Shuil oluline element. Õigesti kasutatuna aitab ta sul jalad alla saada. Kui mõni su kolleeg on liialt õhku täis läinud, laota mulda ta laua ja kabineti ümber. Seejärel saad tunnistada tähelepanuväärset muutust tema suhtumises.

Rohan Candappa

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Classifying clonal growth forms based on vegetative mobility and ramet longevity: a whole community analysis

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Abstract. We measured rhizome branching, clonal mobility, and ramet longevity of 98 meadow plant species. A cluster analysis applied to this dataset revealed nine clonal growth types that differ mainly by the ramet lifespan and vegetative mobility. Then we compared the abundance of these groups of clonal species between the three following plant communities: (1) open, (2) restored and (3) overgrown wooded meadows in the Laelatu-Nehatu-Puhtu Nature Reserve, Estonia. This is the first study where the quantitative values of belowground clonal traits have been measured for all species of a species-rich community. We show that species with annual ramets and with a low vegetative mobility were most abundant in open grasslands. The relative abundance of perennial species with annual ramets was positively correlated with shoot density and species diversity, indicating that high ramet turnover rates combined with a high genet longevity can positively affect species coexistence in meadow communities. Hence, this study provides evidence for the fact that the average values of clonal life-history parameters differ between these communities. Herb communities under forest canopy consist, in average, of species with ramets that live longer and are clonally more mobile than in the communities of open sites.

Key words: branching intensity, growth form, life span, plant community dynamics, ramet, ramet turnover rate, species coexistence, vegetative mobility

Introduction

Extensive clonal plant research conducted over the past decades has yielded a good description and ecological understanding of many stoloniferous and rhizomatous species (e.g., Callaghan *et al.*, 1986; Klimeš, 1992; Kull, 1995a, b; Groenendael *et al.*, 1996). Considerable progress has been made in explaining the mechanisms and benefits of plasticity in clonal growth and architecture (e.g., Hutchings and de Kroon, 1994; Huber and Stuefer, 1997; Skalova *et al.*, 1997). However, approaches to the study of clonal plant morphology and life history from a community perspective have been very rare (Eckert, 1999).

Both meadow and forest floor communities, including semi-natural grasslands, are dominated by clonal perennial plant species (Klimeš *et al.*, 1997). Ramet longevity and the spatio-temporal extent of vegetative spread have been considered to be significant factors both for characterizing and understanding life-history types of clonal plants (e.g., Pokarzhevskaya, 1995; Altesor *et al.*, 1999) and the study of processes affecting community dynamics in herbaceous vegetation (Grubb *et al.*, 1982; Mitchley and Grubb, 1986; Grubb 1990). These two clonal growth traits are major determinants of replacement and dynamics of ramets and of species in plant communities and they form the basis for a phenomenon referred to as 'Carousel model' (Maarel and Sykes, 1993, 1997; Maarel, 1996; Klimeš, 1999), which suggests that in a homogeneous community many (if not all) species can reach virtually all microsites. Ramet lifespan has been used to classify clonal life histories and clonal integration patterns (Jonsdottir and Watson, 1997).

Several clonal growth forms have been distinguished on the basis of combinations of clonal growth traits. These classifications have either aimed at classifying the whole variety of clonal growth characteristics (Klimeš *et al.*, 1997) or they have concentrated on the spatial pattern of clonal growth (*guerilla-* and *phalanx*-type growth; Lovett Doust, 1981; Harper, 1985). Several attempts have been made to distinguish clonal life-history types based on ramet lifespan, longevity of the connecting stem structures (Jonsdottir and Watson, 1997), and on the regeneration strategies (Eriksson, 1997) of clonal plants. A general classification, however, will require detailed and time-consuming measurements of belowground traits (cf. Weiher *et al.*, 1999).

A classification of species on the basis of a few ecologically and functionally significant traits may be useful in order to analyse the specific role of clonal growth in community dynamics and species co-existence. A task for the evolutionary functional ecology of clonal plants is to discover the community-level regularities in the distribution of different clonal life-history types.

In the present study we developed a clonal growth form classification, which is based on measured values of morphological parameters associated with clonal growth. These traits are ramet longevity (i.e. the lifespan of an individual ramet), vegetative mobility (i.e. the distance between a parent and its offspring ramet), and branching intensity (Kull, 1995a, b; Kull *et al.*, 2000). In more detail, ramet lifespan describes how long a ramet occupies a particular microsite in the vegetation. Ramet branching intensity determines the rate of vegetative propagation of a ramet.

In relatively stable communities such as open grasslands, shoots of most species are likely to be short-lived (Maarel, 1996) and species turnover rates are high (Pärtel and Zobel, 1995; Maarel and Sykes, 1997). Plant mobility seems particularly high in open grasslands (Maarel, 1996). Plant mobility is an estimate of the time frame between the appearance and disappearance of above-

ground plant parts in a community. It does not distinguish between vegetative mobility (i.e. mobility by means of vegetative spacers) and mobility through seed dispersal. Plant mobility may alleviate or delay competitive exclusion (Bell, 1984; Herben *et al.*, 1997), which might be particularly relevant for competitively inferior species. Herben *et al.* (1994) have found a negative relationship between the mean aboveground biomass of ramets and plant mobility, suggesting that small plants (i.e. inferior competitors) are more mobile than large plants. These, somewhat contradictory statements, lead us to compare the values of clonal mobility and ramet longevity for the whole sets of species between the communities of different species richness. The communities of wooded meadows serve as a good object for this kind of study, due to the existence of sites of different openness, but otherwise similar in many other respects, close to each other.

Material and methods

Study site

This study has been carried out in the Laelatu wooded meadow at the coast of western Estonia (58°35′ N; 23°33′ E) in 1995. The wooded meadow area, recently 35–40 ha in size (Kukk and Kull, 1997), is a part of the Laelatu-Nehatu-Puhtu Nature Reserve. During the last decades an area of 10–15 ha has been mown once a year. The soil is mesotrophic, lying on Silurian limestone bedrock covered with calcareous moraine. The soil layer is up to 30 cm deep with neutral reaction (pH 6.7–7.0). The content of mobile nutrients in the soil is low to medium (2.5–10.5 mg P_2O_5, 3–16 mg K_2O per 100 g of soil), which is characteristic for natural meadow communities in the boreo-nemoral zone (Krall and Pork, 1970). The mean annual temperature from 1987 to 1997 was 6.3 °C (air) and 7.1 °C (ground); the mean annual precipitation was 600 mm. The rainiest seasons are late summer and autumn with a mean monthly precipitation of 66 mm from July to November and of 38 mm from February to June (Estonian Institute of Meteorology and Hydrobiology; more details in Kukk and Kull, 1997).

We studied three vegetation types, which differ in their history of management: (1) a long time (over 25 years) overgrown wooded meadow, (2) a restored wooded meadow, and (3) an open meadow. According to the traditional management cycle of wooded meadows, these three community types can also be interpreted as successional stages of the same vegetation type. Some characteristics of the studied communities are given in Table 1. The list of main dominant plant species indicates that mesic conditions prevail in all studied communities. Open meadow sites have been mown regularly for at least 200 years. In the restored part of the wooded meadow, brushwood was cut in

Table 1. Characteristics of studied communities

Site	Number of relevés	Number of shoots per m^2	Number of species per m^2	Above-ground phytomass (g m^{-2})	Light penetration coefficient (%)	Main dominant plant species in the community (species with cover ≥10% per m^2)
Open meadow						
1	8	1870	21	664	46	*Rubus caesius*, *R. saxatilis*, *Brachypodium pinnatum*, *Convallaria majalis*, *Angelica sylvestris*, *Filipendula ulmaria*, *Geum rivale*, *Fraxinus excelsior*
3	11	6250	23	443	16	*Molinia coerulea*, *Sesleria coerulea*, *Scorzonera humilis*
4	8	2630	35	327	71	*B. pinnatum*, *Melampyrum nemorosum*, *Leontodon hispidus*, *Serratula tinctoria*, *R. saxatilis*, *Festuca arundinacea*, *Helictotrichon pratense*
5	8	3520	42	301	63	*Pimpinella major*, *S. tinctoria*, *Centaurea jacea*, *Crepis paludosa*, *Co. majalis*, *A. sylvestris*, *Heracleum sibiricum*
6	8	3190	44	262	46	*Le. hispidus*, *S. tinctoria*, *Co. majalis*, *A. sylvestris*, *Ce. jacea*
Restored wooded meadow						
1	8	1780	36	172	86	*Aegopodium podagraria*, *Co. majalis*, *Hepatica nobilis*, *Succisa pratensis*, *Calamagrostis epigeios*
2	8	2350	31	318	73	*Co. majalis*, *Ae. podagraria*, *B. pinnatum*, *M. nemorosum*, *Sarex tinctoria*, *Ca. epigeios*, *C. vaginata*, *Centaurea jacea*
Overgrown wooded meadow						
1	8	715	10	99	ND	*Co. majalis*, *F excelsior*, *Cr. paludosa*, *Molinia coerulea*, *R. caesius*, *Deschampsia caespitosa*, *Stachys sylvatica*
2	8	652	15	128	ND	*Co. majalis*, *F. excelsior*, *C. vaginata*, *R. saxatilis*
3	7	588	14	168	95	*Co. majalis*, *F excelsior*, *R. saxatilis*, *Acer platanoides*
4	6	675	14	167	97	*Co. majalis*, *F excelsior*, *R. saxatilis*, *Ae. podagraria*
5	8	517	18	93	95	*F. excelsior*, *Co. majalis*, *Ae. podagraria*, *Lathyrus vernus*

ND – not determined.

1984 and 1993. In the overgrown wooded meadow site *Fraxinus excelsior*, *Acer platanoides* and *Populus tremula* form a dense tree layer and *Corylus avellana* is the most common shrub.

We carried out a total of 96 vegetation analyses using 1 m^2 plots. Forty-three of them were located in open meadows (from five different open grassland areas), 16 in restored wooded meadows (from two sites), and 37 in overgrown wooded meadows (from five sites; Table 1). For each plot we recorded all species and their relative abundance (%) in the beginning of July (Kukk and Kull, 1997). In addition, the number of shoots was counted in two 0.1×0.25 m^2 subplots within each plot. Light availability was measured above the herb layer by using a fish-eye photographic technique. Light availabilities were expressed as the light penetration coefficient above the herb layer (Anderson, 1964).

Measurements of clonal growth parameters

For each of the 98 clonal vascular plant species found in the vegetation analyses, a minimum of 25 clonal fragments (polycormones) was collected during 1988–1997 In our definition a ramet is a shoot with its branches, produced by one single apical meristem. The ramet also includes the stolon or rhizome connecting it with its parent shoot. The ramet lifespan, vegetative mobility (mm per year), and branching intensity (number of rhizome branches per ramet per year) were measured for each ramet on each clonal fragment.

For instance, in *Carex panicea*, a species with horizontal rhizomes, a ramet consists of the entire rhizome branch and aboveground shoot produced by the same apical meristem. The elongation of *C. panicea* rhizomes is completed by the end of the first growing season after which a vegetative aboveground shoot will be formed. For *C. panicea* the degree of vegetative mobility is thus equal to the length of the rhizome. During the subsequent growing season the same ramet may form a generative shoot. By that time the rhizome and its scale leaves have turned darker in colour. Such morphological changes allow for an estimate of ramet life spans. After fruiting all aboveground parts of the ramet die. In many cases, however, ramets die already at the vegetative stage after the first growing season.

For *Primula veris*, a species with vertical rhizomes, clonal growth parameters were estimated as follows. *Primula veris* forms one rhizome segment in each growing season (Tamm, 1948). Each rhizome segment consists of nodes and short, thick internodes, which are formed at the beginning of the growing season. Internodes formed late in the growing season are much thinner. Such morphological differences enabled us to estimate ramet longevity based on the number of rhizome segments. The apical meristem of *P veris* survives several years. Leaves and flower stalks are formed by lateral buds. After the death of aboveground leaves, the leaf bases remain attached to the rhizome segment. During the subsequent growing season new rhizome segments with new aboveground leaves will be formed. The distance between the current and the previous years' shoot hence reflects the degree of rhizome increment (mm/year)

in this species. As the rhizomes of *P. veris* grow in vertical direction, its vegetative mobility is usually close to 0 even if the increment of the rhizome may reach up to 10 mm per year.

The branching intensity was calculated as the number of rhizome branches per ramet divided by ramet lifespan. For living ramets (ramets with a living aboveground shoot) we did not calculate the branching intensity since we could not estimate ramet lifespans.

Data analysis

Due to a highly skewed distribution of all measured clonal growth parameters, we used the median, maximum and quartile ranges for ramet lifespan, vegetative mobility and ramet branching intensity (Table 2) when classifying clonal growth forms. Our cluster analysis was based on a matrix of presence or absence values of clonal growth characteristics. The Unweighted Pair Group Method using arithmetic means (UPGMA) was applied and the squared Euclidean distance was used as a sample dissimilarity measure.

All statistics were calculated by using SAS (version 6.12, SAS Institute Inc., Cary). Differences in Least Square Means of the relative abundance of clonal growth form groups in different community types were estimated with the GLM procedure using the ESTIMATE statement for comparisons.

We calculated average community-wide clonal growth parameters using weighted averages for each sample plot (weighting according to the relative abundance of species in a sample plot).

The effects of vegetation type, light availability, species richness and shoot density on the community-wide parameters of ramet lifespan and vegetative mobility were assessed by using multivariate ANOVA. The median vegetative mobility of ramets was square root transformed, and the maximum ramet lifespan for each plot was $\log_{10}(x + 2)$ transformed prior to data analysis.

We performed regression analyses to estimate how the ramet lifespan and vegetative mobility changed during succession of wooded meadows. Using the CONTRAST statement in the regression analysis the resulting trend lines were compared for the three vegetation types.

Results

Classification of clonal growth forms

Our cluster analysis (Fig. 1) revealed three major groups of species according to ramet longevity: (*a*) species with annual ramets, (*p*) species with perennial ramets, and (*b*) species with mostly biennial ramets. Within each of these three

Table 2. Median, maximum and quartile range values for measured clonal growth parameters

Species	Ramet lifespan (years)			Vegetative mobility (mm/year)			Branching intensity (ramets/ramet year)		
	Median	Max	Range	Median	Max	Range	Median	Max	Range
Achillea millèfolium	1	1	0	44	202	67	2	6	1
Ae. podagraria	2.5	5	3	232	645	196	0.33	2	0.71
Agrostis stolonifera	1	1	0	2	135	12.8	1	4	1
Alchemilla glaucescens	1	3	3	11.5	25	11.5	1	2	0.5
An. nemorosa	1	1	0	15	38	10	1	3	0
An. ranunculoides	1	1	0	23	32	10	1	3	0
A. sylvestris	5	13	3	0	0	2	0	0	0
Arrhenatherum elatius	1	1	0	3	16	5	0	7	2
Asperula tinctoria	1	1	0	18	237	31.5	1	3	1
B. pinnatum	1	1	0	4	129	10	1	9	3
Briza media	1	4	1	18	161	26	1	5	1.5
Ca. canescens	1	2	0	6.5	210	109	1	8	4
Ca. epigeios	1	2	0	6	275	81.8	1	5	1.75
Campanula glomerata	1	1	0	10	44	13.2	1	2	0
Cam. persicifolia	1	2	1	16	50	29.5	1	2	0
Cam. rotundifolia	1	1	0	23	50	31.2	1.5	5	2.5
C. flacca	2	2	1	30	300	57.5	1	5	0.5
C. ornithopoda	2	2	0	6	23	14	1.25	1.5	0.63
C. panicea	2	3	0	14	210	39	1	2.5	1
C. pulicaris	2	2	0	4	24	6	1	3	1.13
C. tomentosa	1	2	1	8	190	38	0.5	8	1.5
C. vaginata	2.5	4	0	18.5	205	31	1	1.5	0.5
Ce. jacea	1	3	0	8	70	10	1	5	1
Ce. scabiosa	1	7	2	5	30	12.2	0.78	3	0.97
Cirsium acaule	1	1	0	12	31	9	1	3	0
Clinopodium vulgare	1	1	0	16	67	36.5	1	2	0
Co. majalis	5	10	4	240	418	87	0.2	0.4	0.19
Cr. paludosa	1	1	0	7	33	5	1	3	0
Cr. praemorsa	1	1	0	3.5	6	1.75	1	1	0
Dactylis glomerata	1	3	0	4	19	6.5	0.5	5	1
D. caespitosa	1	1	0	1	34	2	1	5	2
Epipactis helleborine	1	1	0	3	6	1	1	1	0
F arundinacea	1	3	0	7	90	16	0	8	1
F ovina	1	2	0	10	70	13	1	3	1
F pratensis	1	5	0	9	130	10	1	5	1
F rubra	1	2	1	5	260	21	1	4	2
Fi. ulmaria	1	3	0	18	41	11.2	1	3	0.38
Fi. vulgaris	2	6	3.75	4	19	2	1	1	0.83
Fragaria vesca stolons	1	2	1	252	465	251	0.67	1	0.17
Fr. vesca rhizomes		6		5	15				
Galium boreale	1	1	0	20	260	35.5	1	5	1
G. mollugo	1	1	0	35	263	48	1	6	1
G. verum	1	1	0	25	190	43	1	8	1
Geranium sanguineum	1	1	0	6	22	4	1	10	0
Geum rivale	4.5	8	2	15	25	6.18	0.71	5	0.2
Helianthemum nummularium	1	1	0	10	210	48	0	11	2
H. pratense	2	6	0	8	40	10	0	2.5	1

Table 2. (Continued)

Species	Ramet lifespan (years)			Vegetative mobility (mm/year)			Branching intensity (ramets/ramet year)		
	Median	Max	Range	Median	Max	Range	Median	Max	Range
H. pubescens	1	2	0.25	14	70	11	1	3	0
Hepatica nobilis	1	7	6.5	0.94	10.5	1.43	0.29	2	0.84
Heracleum sibiricum	3	6	2	0	17	8	1	2.5	0.4
Hypericum maculatum	1	1	0	45	152	49	1	8	1
Hypochaeris maculata	4	7	1	4	12	3.95	0.33	2	0.35
Inula salicina	1	1	0	22	330	38	1	4	0
La. pratensis	1	1	0	65	678	90	1	7	2
La. vernus	1	1	0	6	31	6	1	2	0
Le. hispidus	2	9	2	5.63	30	4.5	0.5	3	0.75
Leucanthemum vulgare	1	3	0	16	83	18	1	4	1
Listera ovata	1	1	0	3	10	1	1	2	0
L. corniculatus	1	2	0	4	70	10	1	6	1
Luzula multiflora	1	2	1	3	20	5.75	0	3	1
Lu. pilosa	1	1	0	4	18	1.5	0	4	1
Maianthemum bifolium	1	4	0	50.5	370	131	1	5	1
Medicago lupulina	1	2	0	6.5	30	6	1.25	6	1
Melica nutans	1	1	0	3	136	12	1	6	2.25
Mo. caerulea	1	1	0	3	13	2	1	2	0
Ophioglossum vulgatum	5	14	3	47	127	28			
Origanum vulgare	1	1	0	20	98	37	1	6	1
Paris quadrifolia	1	1	0	53	90	24.8	1	2	0
Pilosella officinarum stolons		2	2	125	234				
Pi. officinarum rhizomes	1	2		0	22	8	0.5	2	0.9
Pim. major	1	7	1	4	27	6.5	1	3	1.25
Pim. saxifraga	1	6	1	0.5	13	5	1	1.5	0.5
Pl. lanceolata	2.5	9	1.5	0	4	1	0.63	1	0.38
Pl. media	2	3	2.25	0	3	2	0.33	1	0
Poa angustifolia	1	2	1	14	190	38.5	0.5	4	1
Polygala amarella	1	1	0	10	75	10	0.5	1	2
Polygonatum odoratum	1	1	0	26	48	12.8	1	2	0
Potentilla erecta	2.5	5	1.75	0	10	3.15	0.4	1.33	0.67
Primula veris	4	7	2	0	6.33	3	0	2	0.21
Prunella vulgaris	1	1	0	24	144	23.2	1	10	3
Pyrola rotundifolia	3	4	1	67.5	350	120	0.79	1.33	0.54
Ranunculus acris	1	2	1	3	10	2	1	2	0
Ra. cassubicus	1	3	1	2	4	1.5	1	1	0.38
Ra. polyanthemus	1	5	2	3	18	2	1	1	0
R. caesius rhizomes	1	2	0	6	40	11	1	6	1.13
R. caesius stolons		2		280	595				
R. saxatilis rhizomes	1	2	0	8	50	15	1	4	2
R. saxatilis stolons		2		77.5	225				
Sc. humilis		6	2	3	20	21	0.33	2.17	0.5
S. tinctoria	1	3	3	0	11	2	0.83	1	0.51
Se. coerulea	1	5	2	13	86.6	11	1	3	1.5
Solidago virgaurea	1.5	8	4	3.75	11.7	2.5	0.29	2	1

Table 2. (Continued)

Species	Ramet lifespan (years)			Vegetative mobility (mm/year)			Branching intensity (ramets/ramet year)		
	Median	Max	Range	Median	Max	Range	Median	Max	Range
S. sylvatica	1	1	0	100	350	131	2	6	1
Su. pratensis		3		0	0	0	0	0	0
Trifolium montanum	4	17	3	0	25	4	0.24	2	0.63
T. pratense	1	3	1.5	2	30	5	1	4.5	2.38
Trollius europaeus	1	3	2	0	9	2	1	2	0.5
Veronica chamaedrys	1	1	0	90	578	98	1	6	2
V. officinalis	1	1	0	18.5	160	34.8	1.5	4	2.5
Vicia cracca	1	1	0	40	300	80	1	6	1
Vi. sepium	1	1	0	70	420	132	1	6	1
Viola mirabilis	1	3	0	13	72	16.8	1	3	1

groups, species were further subdivided according to their vegetative mobility. These subgroups contained species with (*1*) low, (*2*) medium, (*3*) and high mobility (Table 3).

Distribution of clonal growth forms in different sites of wooded meadow

Ramet lifespan

The relative abundance of species with annual ramets (clonal growth types *a1*, *a2*, *a3*) was higher in open meadows (28%) than in restored and overgrown wooded meadows (16 and 15%, respectively; Table 4, Fig. 2). Species with biennial or perennial ramets showed no significant difference in their relative abundance in open, restored and overgrown sites (19, 23 and 18%, respectively for *b* species, 39, 50 and 38% respectively for *p* species).

Vegetative mobility

The relative abundance of species with low vegetative mobility (clonal growth types *a1*, *b1*, *p1*) was higher in open (39%) and in restored wooded meadows (36%) than in overgrown wooded meadows (20%). In contrast, the relative abundance of species with high vegetative mobility of ramets (clonal growth types *a3*, *b3*, *p3*) was higher in restored and in overgrown wooded meadows (39 and 34%, respectively) compared to open meadows (16%). Species with a medium vegetative mobility (clonal growth types *a2*, *b2*, *p2*) had a higher relative abundance in open meadows (31%) than in overgrown (17%) or restored wooded meadows (14%).

Clonal growth forms in three vegetation types

a1-Species (species with annual ramets and low vegetative mobility) were significantly more abundant in open meadows and in restored wooded meadows

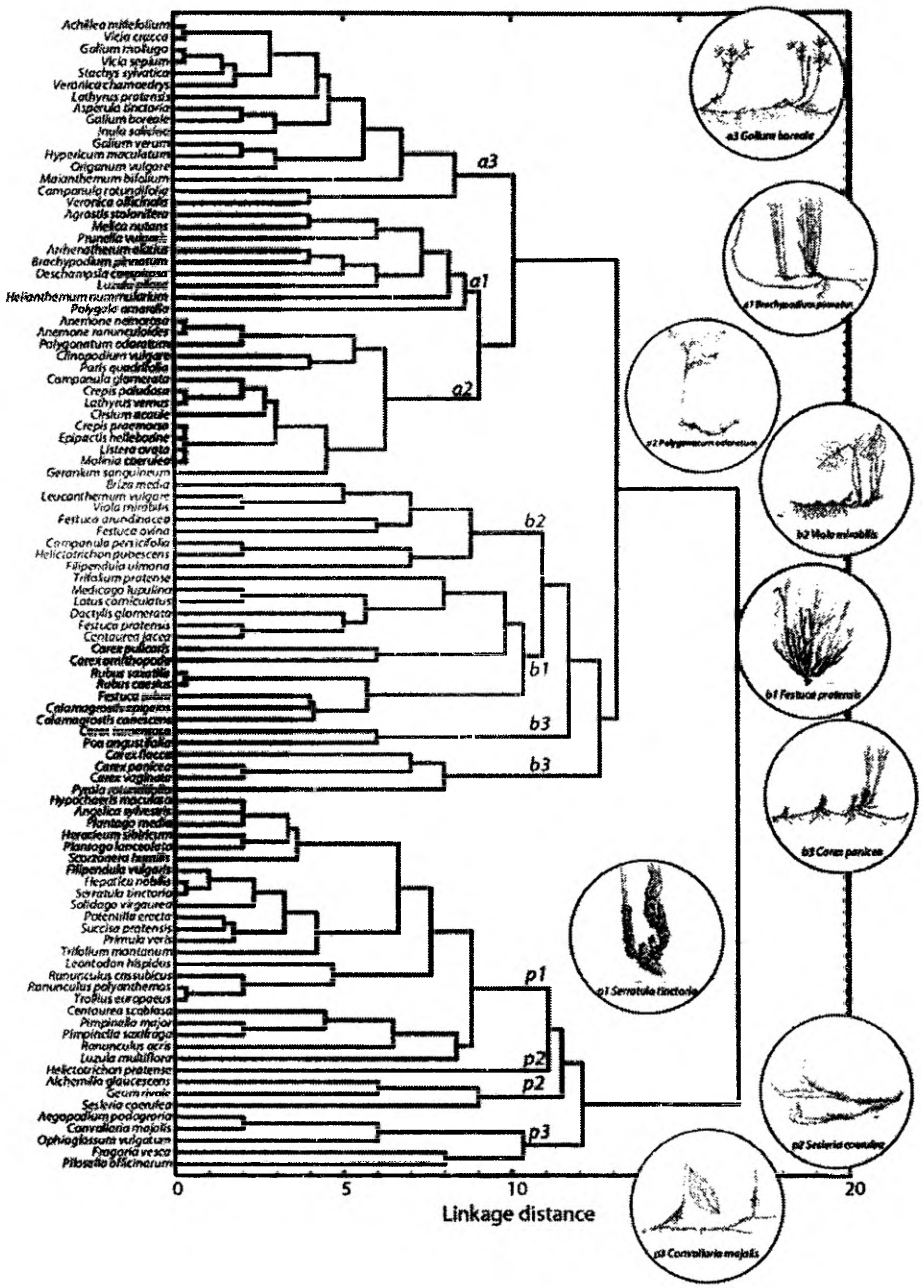

Figure 1. Classification of clonal growth forms according to a cluster analysis. Group: *a* – species with annual ramets, *b* – species with biennial ramets, and *p* – species with perennial ramets. Index: *1* – low, *2* – medium, and *3* – high vegetative mobility.

Table 3. Classification of clonal growth forms, based on ramet lifespan and vegetative mobility parameters

Growth form	Ramet lifespan (years)	Speed of vegetative mobility (mm)	Example species
a1	Annual Med = 1 Max = 1 Range = 0	Low Med < 24 Max 16...144 Range = 1.5...23.2	*Ag. stolonifera, Ar. elatius, B. pinnatum, De. caespitosa, Lu. pilosa, Po. amarella*
a2	Annual Med = 1 Max = 1 Range = 0	Medium Med = 3...53 Max = 6...90 Range = 1...36.5	*An. nemorosa, Cirsium acaule, Ge. sanguineum, La. vernus, Listera ovata, Mo. coerulea, Pol. odoratum*
a3	Annual Med = 1 (1.1) Max = 1 (4) Range = 0	High Med = 18...65 Max = 50...678 Range = 34.8...132	*As. tinctoria, G. boreale, G. mollugo, Hy. maculatum, I. salicina, La. pratensis, Ma. bifolium*
b1	Biennial Med = 1...2 Max = 2 (5) Range = 0...1.5	Low Med = 2...9 (280) Max = 30...275 (595) Range = 5...21(81.8)	*Ca. epigeios, C. ornithopoda, C. pulicaris, Da. glomerata, F. pratensis, F rubra, Me. lupulina, R. saxatilis*
b2	Biennial Med = 1 Max = 2...4 Range = 0...1	Medium Med = 7...18 Max = 41...161 Range = 11...29.5	*Br. media, F. ovina, Fi. ulmaria, H. pubescens, Le. vulgare, Vio. mirabilis*
b3	Biennial Med = 1...3 Max = 2...4 Range = 0...1	High, mobile in the first year Med = 8...68 Max = 190...350 Range = 11...57.5	*C. tomentosa, C. flacca, C. panicea, C. vaginata, Po. angustifolia, Py. rotundifolia*
p1	Perennial Med = 1...4 Max 17 Range = 0.5...6.5	Low Med = 0...5.6 Max = 0...30 Range = 1...21	*A. sylvestris, Le. hispidus, Pl. lanceolata, P veris, Sc. humilis, S. tinctoria*
p2	Perennial Med = 1...4.5 Max = 3...8 Range = 0...3	Medium Med = 8...15 Max = 25...86 Range = 6.2...11.5	*Alchemilla vulgaris, Geum rivale, He. pratense, Se. coerulea*
p3	Perennial Med = 1...5 Max = 2...18 Range = 1...4	High, mobile in the first year Med = (0) 47...252 Max = (0) 127...645 Range = 8...251	*Ae. podagraria, Co. majalis, Fr. vesca, Ophioglossum vulgatum, Pilosella officinarum*
g1	Annual	Absent	*M. nemorosum Linum catharticum*
g2	Perennial	Absent	Seedlings of most tree and shrub species

Median (med), maximum (max) and quartile range (range) of species clonal growth parameters from each growth form group are given. Values in brackets denote exceptional species with stolons (e.g. *R. saxatilis*) or species that can occupy the same patch for several years (e.g. *Co. majalis*).

Table 4. Estimated differences in least square means of relative abundance of different clonal growth forms (class names as in Figure 1) between different community types

Contrast	Annual ramets *a1, a2, a3*	Biennial ramets *b1, b2, b3*	Perennial ramets *p1, p2, p3*	Low mobility *a1, b1, p1*	Medium mobility *a2, b2, p2*	High mobility *a3, b3, p3*
Open-overgrown	<0.005	NS	NS	<0.001	<0.005	<0.005
Restored-overgrown	NS	NS	<0.08	< 0.005	NS	NS
Open-restored	<0.05	NS	NS	NS	<0.005	<0.005

NS – not significant.
Significance of differences in relative abundance is shown. Sample sizes were: open meadow (open) – 43 relevés, restored wooded meadow (restored) – 16 relevés, and overgrown wooded meadow (overgrown) – 37 relevés.

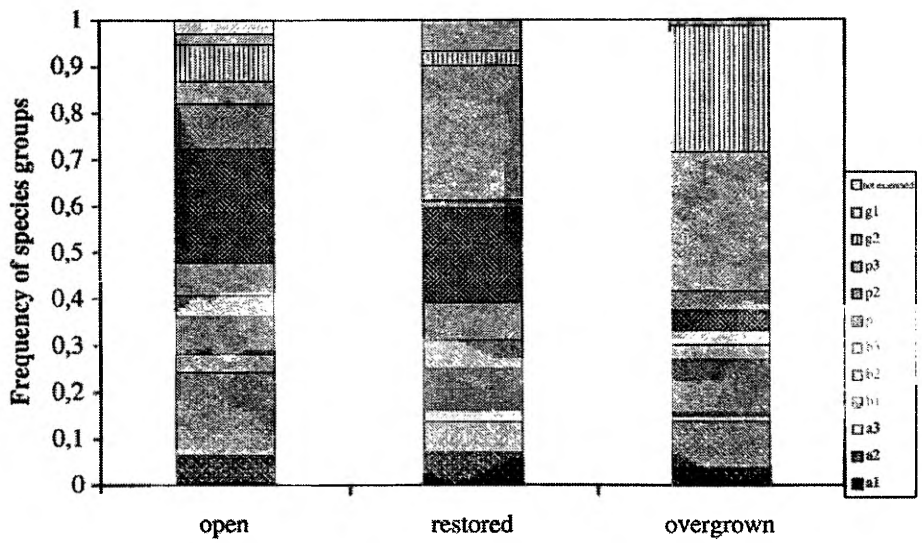

Figure 2. Proportions of clonal growth forms in open meadows, restored wooded meadows, and in overgrown wooded meadows. *g1* Denotes non-clonal annuals and *g2* non-clonal perennials; other symbols correspond to those in Figure 1.

(6 and 7%, respectively) than in overgrown wooded meadows (4%; Table 5, Fig. 2). *a2*-Species (annual ramets with medium vegetative mobility) were more abundant (18%) in open meadows than in restored and overgrown wooded meadows (7 and 10%, respectively).

Although species with biennial ramets (*b*) were equally abundant in the three vegetation types, there was a difference in the relative abundance of *b*-species with low and high vegetative mobility. The relative abundance of *b1*, *b2* and *b3* species in open and in restored wooded meadows were equally low (4–9%). In

Table 5. Estimated differences in least square means of relative abundance of clonal growth forms (class names as in Figure 1) between different community types

	a1	*a2*	*a3*	*b1*	*b2*	*b3*	*p1*	*p2*	*p3*
Open-overgrown	<0.05	NS	<0.01	NS	NS	<0.01	<0.01	<0.01	<0.01
Restored-overgrown	<0.05	NS	<0.09	NS	NS	<0.01	<0.01	NS	NS
Open-restored	NS	<0.05	<0.06	NS	NS	NS	<0.05	<0.01	<0.01

Significance of differences in relative abundance is shown. Sample sizes are as in Table 4.

overgrown wooded meadows the relative abundance of *b3*-species was significantly lower (3%) compared to the other two sites (Table 5, Fig. 2).

p1-Species (perennial ramets with low vegetative mobility) decreased in relative abundance in the sequence of open meadows, restored wooded meadows, overgrown wooded meadows (25, 20 and 4%, respectively; Table 5, Fig. 2). The relative abundance of *p3*-species was significantly lower in open meadows (5%) than in restored wooded meadows (29%) or overgrown wooded meadows (30%; Table 5). *p2*-Species (perennial ramets with medium vegetative mobility) were significantly more abundant in open meadow communities (9%) than in restored (1%) or overgrown (4%) wooded meadow communities.

None of the effects described above did change significantly when absolute abundances were used instead of relative ones.

Relationships between density of ramets and number of species

The vegetation type and the number of species did not have any statistically significant relation with maximum ramet longevity (Table 6). The number of shoots per m^2 had the strongest negative effect on this trait (Table 6, Fig. 3A). All multiple regressions of median vegetative mobility (on number of species, ramet density, and light availability) were statistically significant (Table 6, Fig. 3B). Shoot density showed a strong negative relationship with vegetative mobility.

The slopes of trend lines describing the relationship between community-wide clonal growth parameters were significantly different for open and overgrown wooded meadows as well as for restored and overgrown wooded meadows (Fig. 4, Table 7). No such difference was found between open and restored wooded meadow communities.

Discussion

A cluster analysis revealed large differences between two major groups of clonal herbaceous species present in our study system. The first group con-

Table 6. Results of multivariate ANOVA

Factor	Sums of squares	*d.f.*	*F*	*P*	r^2
Median of vegetative mobility of ramet					
Model	8.75	11	31.08	<0.0001	0.83
Error	1.74	68			
Stage	0.27	2	5.36	<0.01	
Number of species	0.31	1	12.08	<0.001	
Shoot density	0.34	1	13.35	<0.0005	
Light	0.11	1	4.45	<0.05	
Number of species × stage	0.23	2	4.41	<0.05	
Number of shoots × stage	0.56	2	11.02	<0.0001	
Light × stage	0.17	2	3.31	<0.05	
Maximum ramet lifespan					
Model	0.02	11	10.86	<0.0001	0.64
Error	0.01	68			
Stage	0.001	2	2.23	NS	
Number of species	0.0001	1	0.13	NS	
Number of shoots	0.003	1	23.94	0.0001	
Light	0.001	1	9.24	<0.05	
Number of species × stage	0.001	2	13.82	<0.05	
Number of shoots × stage	0.004	2	3.56	0.0001	
Light × stage	0.002	2	7.62	<0.001	

The effects of vegetation type (stage), number of species (per 1 m^2), shoot density (per m^2) and light penetration coefficient to herb layer (light) on maximum ramet lifespan and median of vegetative mobility of community.

tained species with annual and biennial ramets, while the second one was composed of species with perennial ramets (Fig. 1).

Vascular plant species grown in calcareous grassland have been classified in terms of mobility types by Maarel (1996). His five mobility types (constant, local, circulating, pulsating, and occasional species) were based on above-ground estimates of cumulative species frequency in a series of small subplots. Vegetative mobility (i.e., mobility by clonal propagation) and mobility by means of seed dispersal were not separated from each other in that study, thereby confounding different processes underlying the spatio-temporal dynamics of ramets and genets in communities. In the classification mentioned above, species with a low vegetative mobility, such as *Plantago lanceolata* and *Lotus corniculatus*, shared the same group (*circulating species*) as species with long rhizomes (e.g., *Achillea millefolium*, *Galium verum*). The high turnover rate of *Pl. lanceolata* and *L. corniculatus* in calcareous grasslands, however, is a likely result of frequent regeneration from seeds (cf. Pärtel *et al.*, 1998).

According to our study, the relative abundance of species with a short ramet lifespan (group *a*) and low vegetative mobility increased with shoot density. Another relationship between different community-wide parameters of clonal

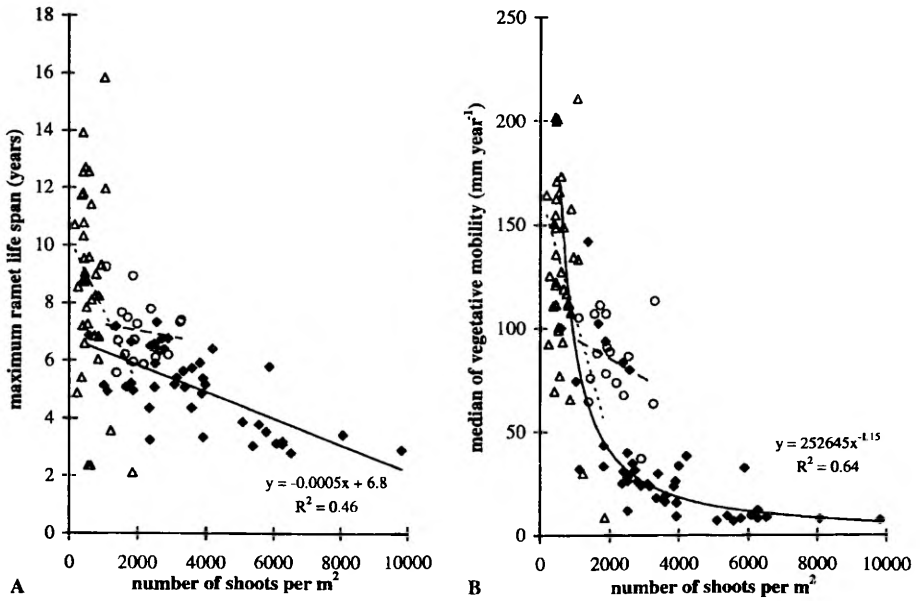

Figure 3. Weighted average of (A) ramet lifespan and (B) vegetative mobility in relation to shoot density in our sample plot communities. Diamonds, circles and triangles represent open meadows, restored wooded meadows, and overgrown wooded meadows, respectively. The R^2 value of the regression line and the equation are shown for open meadow plots only.

growth shows that in overgrown wooded meadows, maximum ramet longevity increases with increasing vegetative mobility (Fig. 4). The latter trend can be attributed to the relatively higher frequency of species from growth form *p3* in overgrown wooded meadow sites. Good examples are *Convallaria majalis* and *Aegopodium podagraria* with ramets developing aboveground shoots after rhizome formation, and which can persist in the same patch for a long time (Kivenheimo, 1947; Rysin and Rysina, 1987). In shade, where the overall number of ramets per unit area is lower than in open sites, this persistence will lead to a dominance of such species.

Mowing of open grasslands results in a disproportional removal of tall plants and hence equalizes size hierarchies and reduces the asymmetry between plants in their competition for light (Lepš, 1999). Inferior competitors are thus more likely to establish in new gaps created by mowing.

Herben *et al.* (1997) have suggested that high turnover rates may promote coexistance of a large number of plant species. Also, in some other studies the high mobility was related to high species richness (Sykes *et al.*, 1994). Contrary to that conclusion, Klimeš (1999) found low plant mobility in species-rich grassland in S. Moravia (Czech Republic). In the latter study plant mobility was very low, which indicates that many species either kept their positions over many years or established in micro sites that had previously been occupied by

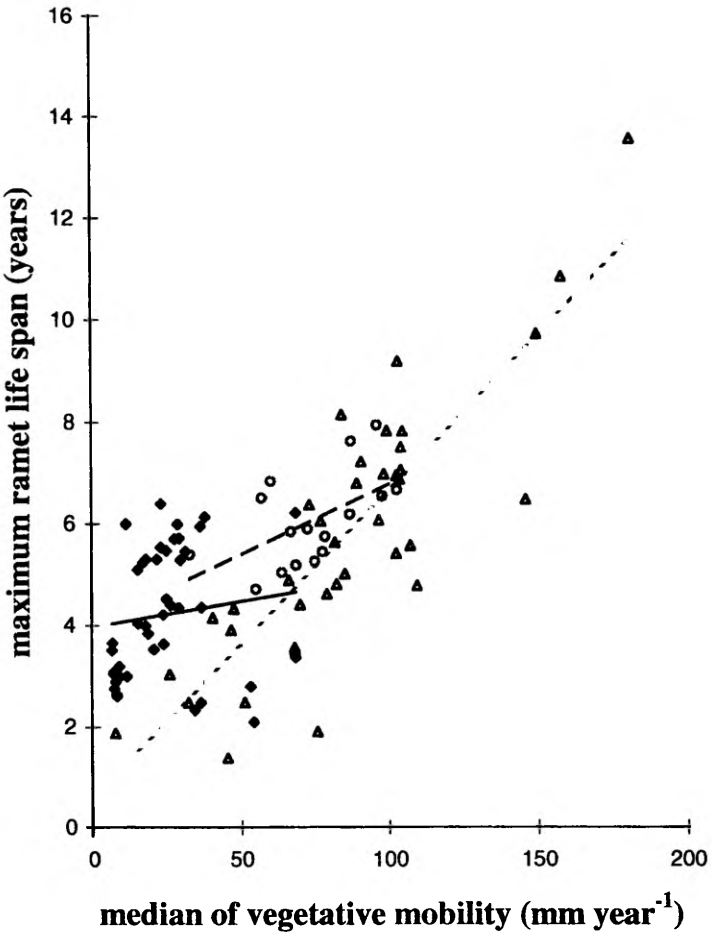

Figure 4. Relationship between weighted averages of maximum ramet life span and median vegetative mobility. Diamonds, circles and triangles represent open meadows (solid regression line), restored wooded meadows (widely dotted regression line), and overgrown wooded meadows (dotted regression line), respectively.

ramets belonging to the same species. At that point we want to emphasize that high plant mobility and high ramet turnover rate are separate things. High ramet turnover rate means that ramets are short-lived and they replace each other within a short period of time, irrespective of their vegetative mobility.

According to our results, which are based on the measurements of the clonal growth characteristics of all species of a community, we can clearly state that, when transforming a temporal forest into a meadow, the clonal mobility of the herb community and the average lifespan of ramets decreases, which, in turn, leads to a higher turnover rate of ramets. This may possibly contribute to the higher potential species richness of the community.

Table 7. Regression of weighed average of maximum ramet lifespan on weighed average of median of ramet vegetative mobility (mobility) in different community types (stage)

Factor	Sums of squares	*d.f.*	*F*	*p*	r^2
Maximum ramet lifespan					
Model	0.02	5	30.86	<0.0001	0.63
Error	0.01	90			
Stage	0.004	2	13.84	<0.0001	
Mobility (stage)	0.003	3	19.76	<0.0001	
Contrast					
Open vs. overgrown	0.004	2	13.58	<0.0001	
Open vs. restored	0.0006	2	2.01	NS	
Restored vs. overgrown	0.001	2	4.53	<0.05	

The comparison of trend lines (contrast) in different community types was obtained by using the GLM Contrast method.

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"I can't believe I was stupid enough to do these experiments on clonal plants."

Deborah E. Goldberg
Kuusamo, August 2003.

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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

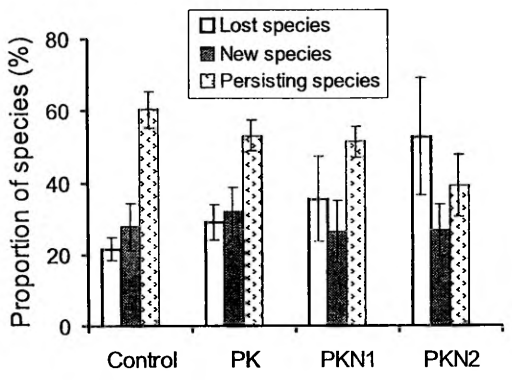

Fig. 1. The proportions of species present in the plots throughout the experiment (persisting species), species that disappeared from the plots in the course of the experiment (lost species), and species that invaded the plots during the experiment (new species). The average of three replicates ± standard 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

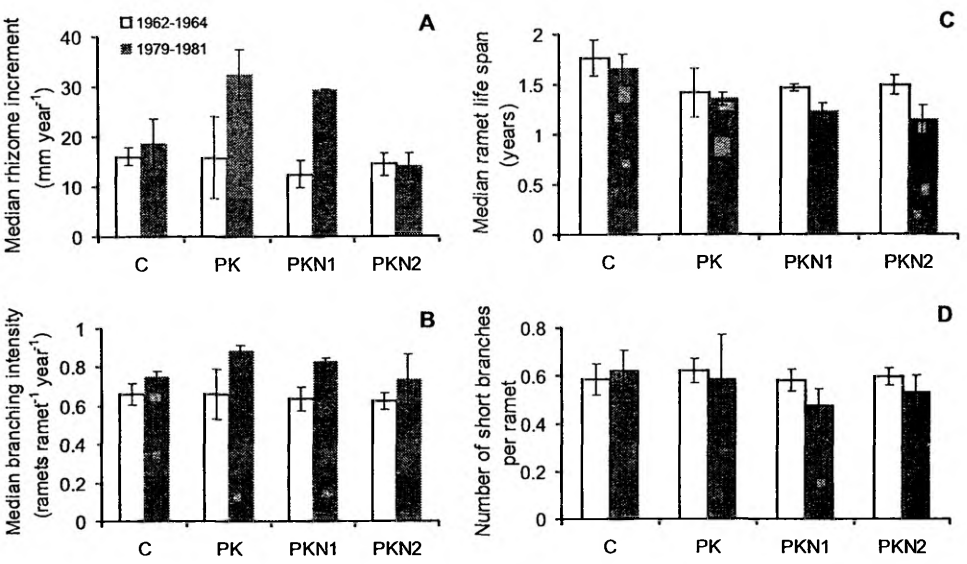

Fig. 2. The weighted average of the median of yearly rhizome increment (A), branching intensity (B), ramet life span (C), and number of short branches per ramet (D) at the beginning (1962–1964) and at the end (1979–1981) of the experiment. The average of three replicates ± standard deviation is presented.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

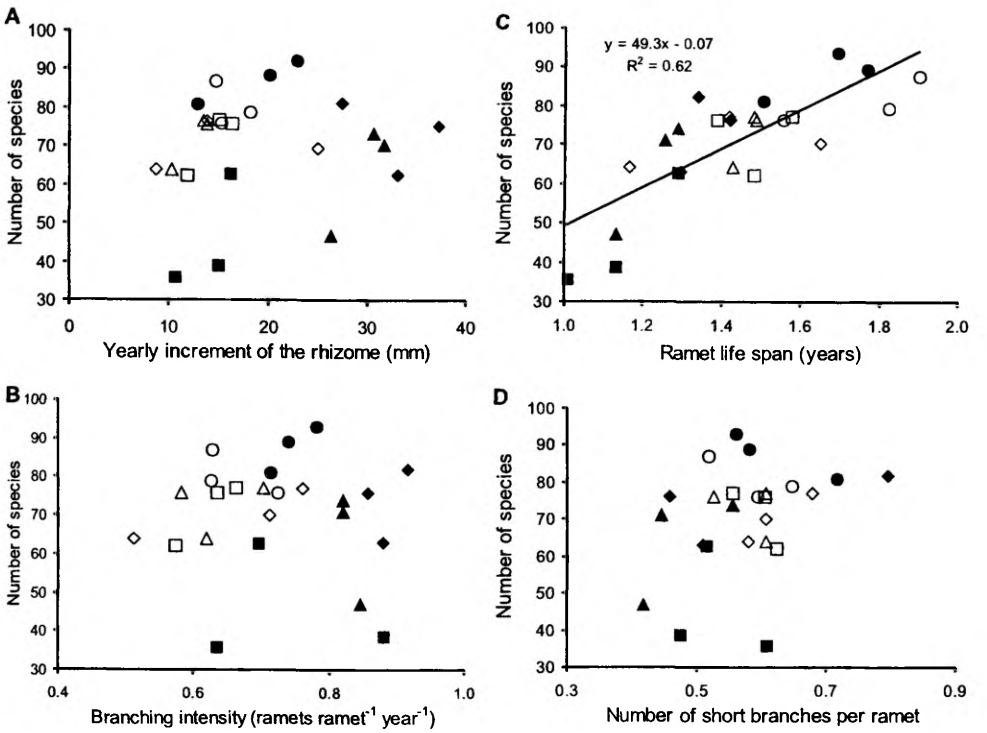

Fig. 3. The relationship between the number of species found in the plot and the corresponding weighted average of the median of yearly increment of the rhizome (A), branching intensity (B), ramet life span (C), and number of short banches per ramet (D). Each point in the figure denotes a separate plot 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

In an old silverline
I was yours, you were mine
I was hoarse, you were mean
We designed drum machines

They made sounds much like drums
I was young you were dumb
Now you're older and I'm wiser
We design synthesizers

Stephin Merritt / The 6ths

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A COMPARISON OF PLANT COMMUNITIES ON THE BASIS OF THEIR CLONAL GROWTH PATTERNS

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ABSTRACT

We compared the plant communities on the basis of the clonal growth characteristics of all constituent species. The parameters used were community average ramet life span, rhizome branching, and clonal mobility. The study included the herbal communities of forests, wooded meadows, and open meadows in Laelatu, Estonia.

We found that average ramet life span in community was decreasing with increasing biomass of the herb layer. Yet, ramet density was the most sensitive characteristic of vegetation co-varying with both environmental factors and several other traits of vegetation including clonal growth parameters. Independent of the effect of environmental factors the species density was positively correlated with ramet density, while ramet density also was positively correlated with rhizome branching.

There were several differences between these and other relationships in different communities. Species density was positively correlated with ramet life span only in open sites and negatively correlated with rhizome increment only on wooded meadow sites.

No evidence was found for hypothesis that the species-rich communities may consist of species with more contrasting mobility than the species-poor communities. Instead, we found that in forest communities capability to forage for light is favoured while in unmown meadows competitively strong phalanx growth form is advantageous. We found that ramet turnover increases and vegetative mobility decreases with increasing species diversity. However, these results strongly depend on the type of studied community.

We conclude that exploration of the variation of clonal growth parameters of plant communities improves the understanding of reasons behind vegetation patterns, since these parameters refer to the causal processes responsible for the formation of community structure.

INTRODUCTION

There are several plant communities, which are extremely species-rich and consist mainly of clonal plants (Kull & Zobel 1991, Kukk & Kull 1997, Klimeš1999). It is not known to what extent species richness is affected by the properties of clonal spreading or the way of reproduction of constituent species in a certain community. There have been a few attempts to estimate the role of species turnover in species coexistence (e.g. Herben et al. 1994, Klimeš 1999) and the relationship between species richness and clonal growth characteristics of constituent species in a community (e.g. Sammul et al. 2003). However, it is basically unexplored if the abovementioned relationships exist at all (Herben et al. 1997, Klimeš 1999).

There have been numerous studies concerning the variation of clonal growth characteristics of species or individual clones along environmental gradients (see Hutchings & de Kroon 1994, de Kroon & Hutchings1995 for a review) and possible consequent foraging behaviour (Sutherland & Stillman 1988, Cain 1994, Oborny 1994, Piqueras et al. 1999). It has been shown that the ability to change the clonal growth in response to changing environment is species-specific, and there are species that do not have such an ability (de Kroon & Hutchings1995). Moreover, there are even less species which are plastic enough to respond to environmental heterogeneity at the scales the latter occurs in nature (Hutchings & de Kroon 1994, Stuefer 1996).

Similar studies on community level, i.e. the studies where clonal growth of all species in the certain community were estimated and compared to some other community (e.g. Pokarzhevskaya 1995, Tamm et al. 2002) or compared with the same community after some kind of perturbation (e.g. fertilization in Sammul et al. 2003), are very few. Mostly some permanent plot has been mapped with high spatial resolution and the spatio-temporal dynamics of shoots in this plot has been observed (e.g. Rusch & van der Maarel 1992, van der Maarel & Sykes 1993, Herben et al. 1994, Pärtel & Zobel 1995). These studies have revealed that there exists considerable turnover of species in both spatial and temporal scale, and such mobility or turnover (if detected by data on shoots it will be further on in the text referred to as shoot mobility or shoot turnover, while the terms vegetative mobility and clonal mobility will be preserved for describing the ability of a clone to move in space using its vegetative organs (rhizomes, stolons etc.) and change the location of its shoots) differs between species (Thórhallsdóttir 1990, Rusch & van der Maarel 1992, van der Maarel & Sykes 1993, Herben et al. 1994, Law et al. 1994, Sykes et al. 1994) and between different communities (Herben et al. 1994, Pärtel & Zobel 1995). It is shown that disturbance, such as drought, may enhance shoot mobility (van der Maarel 1996) and that higher shoot mobility can be found in communities with higher species richness (Sykes et al. 1994). On the other hand, Pärtel & Zobel (1995) found that during successional changes the speed of shoot mobility did not

change, Herben et al. (1994) found fairly similar shoot mobility in communities with different species richness and Klimeš (1999) showed that low shoot mobility does not contradict high species richness.

The method described above suffers from inability to discriminate between different types of reproduction and mobility. In order to quantify the abundance of different types of reproduction and/or clonal growth in different communities a more mechanical approach for community analysis is necessary. Furthermore, the method described above, is not applicable in species-poor systems, where most of the shoots belong to a few species and therefore the real extent of shoot turnover and mobility of ramets remains undetected. And lastly, this method is rather time-consuming.

Another method for comparison of community-level differences in clonal growth (Tamm et al. 2002, Sammul et al. 2003, see also Kull 1995) assumes that the parameters of clonal growth are species-specific and do not change with changing environmental conditions substantially. The variation of the parameters can be treated as a separate variable with its own ecological meaning. The community-level estimate of clonal growth can be achieved by calculation of weighed average of the clonal growth parameter with some estimate of the abundance of each constituent species in the community as a weight (e.g. Sammul et al. 2003).

For several species the assumption of constancy of parameters of clonal propagation is an oversimplification and does not hold. However, it would be too laborous to estimate all clonal growth characteristics for each species in each natural community separately in a manner that would provide decent statistical reliability. The advantage of using this method is that the relationship of each clonal growth trait to environmental variables can be evaluated separately, thus providing the understanding of the function of each trait in dynamics of communities.

The average clonal growth in community may change with changing environmental conditions in several ways. For example, species with some distinct values of some parameter of clonal growth may prevail in certain conditions. This may result, for example, in increased level of vegetative mobility with increasing abundance of legumes in community (Sammul et al. 2003) or in decreased share of vegetatively mobile species in high alpine communities, where long runners can be damaged by moving soil during cold winter (Pokarzhevskaya 1995). On the other hand, some communities may consist of species with similar values of clonal growth parameters, whereas some other communities may consist of species with fairly different values of these parameters and, thus, leading to the increase in the variation of clonal growth parameters among coexisting species.

All these presumptive differences are caused by changes in species composition but may well also be the concurrent reason of changing species composition. Either way, the changes in mobility pattern of ramets in community affect the dynamics of the community (Herben et al. 1993, Sykes et

al. 1994, Herben & Hara 1997). It has been shown that interspecific difference in mobility promotes coexistence in modelling studies (Bell 1984, Caswell & Cohen 1991) as well as in experimental communities (Schmid & Harper 1985). If the inferior competitor is more mobile than the superior one, it may avoid competitive exclusion by moving to more favourable spot (Klimeš 1999).

In this study we are going to estimate the relationship between community clonal growth and a few important characteristcs of the community (aboveground biomass of the herb layer, light availability to herb layer, mowing frequency, species density, and ramet density). We specifically address our attention to the few relationships found in earlier studies, or hypothesized to be present:

A) is the high mobility of species characteristic to communities with high species richness?
B) Are the species richness and proportion of species with long life span of ramets in community positively correlated?
C) Do the species-rich communities consist of species with more contrasting mobility than species-poor communities?

We will consider in our analyses that all community-wide clonal growth parameters are dependent on and covary with species composition. Therefore we will first estimate the influence of main environmental variables (mowing, community productivity, light availability) on parameters associated with changing vegetation. Further on, we will estimate the relationships between average clonal growth in community, ramet density, and species density that are not caused by covariation with environmental variables.

METHODS

Study area

Laelatu wooded meadow is located on the western coast of Estonia (lat. 58° 35' 15" N, long. 23° 33' 00" E) on the West Estonian Lowland. It forms part of the Laelatu-Puhtu-Nehatu Nature Reserve. The total area of the meadow is 150 ha, but today only ca 15 ha are mown regularly (Kukk & Kull 1997). The area has been exploited for at least 300 years for hay cutting. There are no reports to the effect that this area has ever been grazed. The area emerged from the sea 1000–2000 years ago (Sepp & Rooma 1970) and belongs to the boreo-nemoral zone. The soil is rendzic leptosol with a pH of 6.7–7.2 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).

Mean temperature for July is 17°C and for January –5°C. Annual mean temperature is 6.3°C in the air and 7.1°C on the ground. Mean annual precipitation is 500–600 mm, the most rainy seasons are late summer and autumn.

The vegetation of 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 flora of vascular plants in Laelatu wooded meadow and adjacent areas comprises 470 species, while 225 species are known directly from the wooded meadow (Kukk & Kull 1997). The bryoflora of Laelatu consists of 96 species (Ingerpuu et al. 1998). The vegetation belongs mostly to the *Sesleria coerulea – Filipendula hexapetala* association (Krall & Pork 1970). The tree layer (crown projections) covers on average 30–50% of the ground surface and consists of *Quercus robur* L., *Betula spp.* L., *Fraxinus excelsior* L., *Populus tremula* L. a.o. (Kukk & Kull 1997; nomenclature follows Kukk 1999). Abandoned wooded meadow areas are nowadays covered with deciduous forests of different age. Dominant tree species in forests are *Betula spp.*, *Fraxinus excelsior*, *Populus tremula* and *Alnus incana* (L) Moench.

The study area provides wide range of several environmental gradients in a relatively small area. The land that has rised from the see earlier has shallower and dryer soil. In case these spots are not overgrown with forest, they have lower productivity and mostly also higher species density. Lower parts of the meadow are moister, have higher productivity and lower species density. Variable cover of trees absorbes different amount of light and provides different level of direct sunlight to the ground layer.

The gradients of available light, soil moisture and productivity are related to each other. Together with the history of the management of the area they determine local species density Spots with continuous mowing (once a year) for over 40 years, medium moisture conditions, low (but not the lowest) productivity and tree cover less than 50% are the most species rich (over 60 species of vascular plants per square meter).

Vegetation censuses

A total of 104 vegetation analyses were carried out using 1 m^2 plots. The plots were located in 13 different sites: 5 sites of deciduous forests and overgrown wooded meadows, 4 sites of wooded meadows with medium tree cover, and 4 sites of open or totally devoid of trees calcareous meadows. The communities were chosen to provide the full gradient of direct sunlight available to ground layer. The list of plant species indicates that mesic conditions prevail in all studied communities.

Mostly 8 plots per community were analysed (Table 1). In each plot all species were recorded and their cover was estimated. In addition, the number of ramets (ramet is a shoot with a part of the stolon or rhizome connecting it with its parent shoot) was counted in two 0.1×0.25 m^2 subplots within each plot. The subplots were located in opposite corners of the 1 m^2 plot and 15 cm inside from both nearest sides of the plot. All shoots in the subplot were cut close to the ground layer, collected, dried at the 80°C for 48 hours and weighed with an accuracy of 0.1 g to estimate the phytomass of the community. Light availability to the ground layer was measured above the herb layer by using a fish-eye photographic technique. Light availabilities were expressed as the light penetration coefficient (Anderson 1964). In each community also the frequency of mowing was recorded using information from the managers of the area.

Data on clonal characteristics of species

Clonal fragments (polycormons) of 120 most abundant species of Laelatu wooded meadow were excavated between 1988–1997 for measurement of clonal growth parameters. Most excavations took place in 1995–1996. 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.

Using scars from dead shoots on rhizomes as well as size and morphology of internodes and nodes on rhizomes, for all ramets their age and annual increase of their rhizome parts were measured and the number of rhizome branches per ramet was counted (Kull 1995, Tamm et al. 2002, Sammul et al. 2003; detailed results of these measurements will be published elsewhere and are partly presented in of abovementioned references). Due to differences in formation of nodes and internodes in different seasons it is possible to determine yearly growth of the rhizome. In most cases the rhizome is formed within the first year of the ramets life. If the ramet is perennial it mostly does not move horizontally after the first year. In spring the internodes of the rhizome are commonly longer and thinner than internodes that have grown later in the year. They also differ in their colour. Very often there are remainders of old leaves on the rhizome, which shows the place where the shoot has been growing. If the ramet is annual, each separate rhizome branch has been formed within one year. Such morphological differences allow to estimate ramet life span and yearly growth of the rhizome (see also Tamm et al. 2002, Sammul et al. 2003).

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.

From the measurements of clonal fragments the following parameters were calculated for each species: median of ramet lifespan, median of number of

branches per ramet, median of branching intensity (number of rhizome branches per ramet per year), median of rhizome increment per year, and proportion of short (<1 cm) branches per ramet. Median was chosen instead of the average due to very asymmetric distribution of these variables within species. It was impossible to transform the variables to fit normal distribution and therefore it was necessary to use distribution-free parameters.

For several species found in vegetation analyses with low frequency and small biomass share, clonal fragments were not excavated. Whenever possible, the parameters of the clonal growth of these species were estimated on the basis of 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 similar communities.

For 39 species out of 166 that were found in relevés, it was not possible to measure all parameters of clonal propagation, or else sample size for measurement was too small (<5). In each $1m^2$ plot the sum of the cover for these species constituted less than 5%. The parameters of clonal propagation for these species were treated as missing values in data processing.

Data analysis

For each plot we calculated the weighed average of each clonal growth parameter (M_{pj}) as:

$$M_{pj} = \sum a_i p_{ij} \qquad \text{Eq. 1.}$$

Here a_i is the percent cover (from 0 to 1) for species i in the plot and p_{ij} is the value of j-th clonal growth parameter for species i.

We measured the difference in extent of clonal mobility in coexisting species with a coefficient of variation of medians of rhizome increment of all species in one relevé. The coefficient of variation was chosen since it is a variance estimator independent of the values of the sample mean. To also correct for possible bias associated with different sample sizes we used following correction (Sokal & Rohlf 1995):

$$CV_{increment} = (1 + 1 / 4n)\,(St.Dev._{increment} \times 100 / Y_{increment}). \qquad \text{Eq. 2.}$$

Here $CV_{increment}$ stands for corrected coefficient of variation of median rhizome increment per plot, n is the sample size, $St.Dev._{increment}$ is the standard deviation of rhizome increment in one plot, and $Y_{increment}$ is the mean of rhizome increments of all species found on a plot.

To test for general relationships between different environmental variables and vegetation characters (incl. community-wide parameters of clonal growth) we built a squared correlation matrix with Pearsons r and probabilities of error

(p-level). To correct for mass effect we used the Bonferroni type correction with Dunn-Šidák method (Sokal & Rohlf 1995) and obtained the critical p-level (experimentwise error rate) using following equation:

$$p_{critical} = 1 \quad (1 - 0.05)^{1/k} \qquad \text{Eq. 3.}$$

Here 0.05 is the original level of probability of type I error and k stands for the number of comparisons below the diagonal of the squared correlation matrix. To obtain normal distribution the number of species per plot was square-root transformed prior to analyses.

General linear mixed model as implemented in procedure MIXED of statistical package SAS (version 6.12, SAS Institute Inc., Cary) was used to estimate impact of biomass, light availability, mowing regime, and site on species density, ramet density and community clonal growth parameters. Due to high association and lack of overlap in factors mowing and site they were combined into a new factor named *HABITAT*. This factor comprised of seven different levels – forest sites with no mowing, open sites with mowing frequency 0.1 times/year,open sites with mowing frequency 0.2 times/year, open sites with mowing frequency once a year, wooded meadow sites with mowing frequency 0.5 times/year, wooded meadow sites with mowing frequency 0.6–0.7 times/year, and wooded meadow sites with mowing frequency once a year.

The following model was tested:

$$Y = \mu + a_1 HABITAT + a_2 L + a_3 L^2 + a_4 B + a_5 B^2 + a_6 LB. \qquad \text{Eq. 4.}$$

Here Y denotes dependent variable, μ is intercept, L stands for light penetration coefficient, and B is biomass, and a_1 to a_6 are coefficients. Factor *SITE* was added to the model as a random factor. Factors L, and B were nested in *HABITAT* while factors *SITE* and *HABITAT* were nested in type of the community. Type 3 test of fixed effects was used with the iterative Restricted Maximum Likelihood (REML) procedure to estimate the effect of variance components.

To test for dependencies of variables on biomass, light availability and different mowing regimes within one type of the community as well as for differences in average values of variables between the three types of community we used statement ESTIMATE. In addition the differences in least squares means were calculated, but since these yielded similar results they are not presented here.

We also estimated the intrinsic relationships between community clonal growth parameters, ramet density and species density. For that we calculated Pearsons partial correlation coefficients with light, biomass, their squared effects and combined effect (i.e. all continuous factors included in the model (Eq. 4)) kept constant as partial variables. This was done for the whole dataset

and for each of the three community types separately. To the resulting matrixes of partial correlations we applied the correction of error rates (Eq. 2) as described above.

RESULTS

We found that over 2/3 of the 36 calculated correlation coefficients between environmental factors and vegetation variables were statistically significant (Table 3). All three studied community clonal growth parameters were correlated with biomass, light availability, and ramet density Only the rhizome increment was correlated with species density and mowing frequency (both corrrelations were negative, Table 3).

There were only a few effects of fixed factors on studied parameters of vegetation and average community clonal growth parameters. The ramet density was dependent on all factors included in the model (Table 4). Species density was significantly dependent only on *TREATMENT*, although there were marginal dependencies also on light availability and interaction term of light and biomass (Table 4). Of the studied community-wide clonal growth parameters only the effect of biomass on ramet life span was statistically significant ($F_{7,56}$=2.23, P<0.05). The marginal effect of square of biomass ($F_{7,56}$=1.96, P=0.077) showed that this relationship is slightly non-linear. No other effects of fixed factors were detected. Random factors site and intercept were never significant.

We detected the effects of mowing frequency, biomass, and light availability on ramet density in open sites (Table 5). We also found biomass of forest floor positively affecting average ramet life span and average rhizome increment in the community (Table 5). The only direct effect of the type of the community on average values of vegetation parameters and clonal growth characteristics was that in open sites the shoot density proved to be higher than in other community types ($|t_{56}|$=4.72, p<0.0001 for both comparisons).

The coefficients of partial correlation between studied variables for the whole dataset are given in Table 6. We found that all three community clonal growth parameters are correlated with each other and coefficient of variation of rhizome increments of coexisting species is negatively correlated with branching intensity. We also found a positive partial correlation between species density and ramet density, and between ramet density and branching intensity (Table 6).

When we analysed three types of communities separately, we found that there is a positive partial correlation between branching intensity and ramet density in forests (r=0.61; p=0.0002), and between ramet life span and species density in open sites (r=0.56; p=0.0014). We also found a negative partial correlation between community vegetative mobility (rhizome increment) and species density in wooded meadow sites (r=–0.54; p=0.0036).

DISCUSSION

The correlation between environmental factors, parameters of vegetation and clonal growth characteristics of community (Table 3) is to be expected, since environmental factors influence vegetation composition and calculation of clonal growth of the community depends on the latter. However, it is surprising that these relationships are not supported by the analyses with more sophisticated statistical methods. It could be that we missed some important driving factor of the composition of these communities. Though, since the sites were located in very similar soil conditions, and light, as the most important above-ground factor was also taken into account, it is more probable that the variation within individual sites, the covariation of different factors and lack of the overlap of the latter in different community types created the situation were no effect of single factor could have been detected, despite many putative relationships. This idea is also supported by the fact that there were hardly any statistically significant differences found between individual habitats or even between three types of communities involved in this study. Yet, the differences were remarkable (Tables 1–2). It is unfortunate but unavoidable that any natural gradient has several dependencies between different factors. Still, it is not always possible or even sensible to perform only experiments where most of random environmental variation can be reduced. Even more so, when we still do not know how the studied parameters vary in nature, as is the case with average clonal growth in the community.

In our previous study of changes in community clonal growth after fertilization (Sammul et al. 2003) we found that with fertilization both vegetative mobility in community and branching intensity increase, although this result is dependent on the level of nitrogen limitation and abovementioned clonal growth parameters increase at most if N-limitation is strong. The productivity of the herb layer of communities studied here is more complexly determined and both soil and light conditions influence it. We found that increasing biomass of herb layer is in this study negatively correlated with both vegetative mobility and branching intensity of the whole community (Table 3, Figure 1). However, this is not a mere effect of productivity, as shows the analysis of a mixed model. Biomass covaries with light availability and is influenced by mowing regime. Consequently, this results in differences between communities and individual sites. We found that in the sequence: open sites, wooded meadow sites, and forest sites, there is considerable increase of clonal mobility and decrease of branching intensity in the community (Table 2). In meadows high branching may be an effective way to ensure that genet gains access to resources. There is no need to move around more than necessary for simple spread and for avoiding interactions with stronger competitors, i.e. it is not directly necessary for survival of the genet. Branching also helps to avoid overtopping by other plants in meadows, since the height to width ratio of size

of genets can be reduced by increasing number of ramets within genet. In forests such strategy would be less profitable, since below the trees it is vital to find the spot where there is enough light available.

It can be concluded from many studies that the foraging behaviour of plants is mostly related to the heterogeneity of light conditions (e.g. Dong 1994, Hutchings & de Kroon 1994, de Kroon & Hutchings 1995). In forest sites and wooded meadow sites light conditions are very heterogeneous. In general, species with plastic growth, capable of changing their clonal growth pattern in time and space (i.e. with ability to "forage" Slade & Hutchings 1987, Sutherland & Stillman 1988) should have an advantage in communities where resources are located heterogeneously (Hutchings & Wijesinghe 1997). Our results show that in wooded communities, where light is very heterogeneously distributed, there are more species with high mobility and long ramet life span. The ability to move long distance is helpful for finding a suitable place considering the scale at which the heterogeneity of light occurs in forested areas (see also Stuefer 1996). It is possible that high absolute mobility values accord with high plasiticity of mobility. However, the effectiveness of morphological plasticity in foraging for sunflecks in forest understorey has even been questioned before (Dong 1994, but see Macdonald & Lieffers 1993). Regardless, the growth form which allows for plants to move long distance vegetatively during their first year of life and then inhabit chosen spot for a long time seems to suit well into the forest environment, where light gaps are spatially separated, but relatively long-lasting.

The variability of community clonal growth parameters in different plots is very high in forest (Figures 1–3). This may have to do with low number of species found in forests, which makes the results of calculation of weighed averages dependent on presence or absence of few species with high mobility and long life span of ramets (such as *Aegopodium podagraria* L. or *Convallaria majalis* L.). Forest floor mostly is covered by tree seedlings which do not live long, do not move, and at the same time do not have much biomass. Whenever the herbaceous plants are present, however, they tend to dominate and increase the biomass of forest floor community. If there were more species this variation between individual plots would be "smoothed" However, there are not many species which can grow in low-light conditions of forest understorey. Therefore, if the species with high mobility and persistent ramets are often dominating when present, it should also reflect the suitability of their growth form into these conditions.

There is not much information available yet on how clonal growth or vegetative mobility may influence species interactions. Almost always the species which take advantage of undisturbed competition and changing environmental conditions are clonal (e.g. Bobbink & Willems 1987, Soukupová 1992 and references therein). Yet, the most species-rich communities also consist mainly of clonal species (Kull & Zobel 1991, Kukk & Kull 1997, Cantero et al. 1999, Klimeš et al. 2001). It has been hypothesised that if the

inferior competitor is mobile it may avoid competitive exclusion by moving to a more favourable spot and and, thus, contrasting mobility of species may enhance their coexistence (Schmid & Harper 1985). In this study we found no evidence for the hypothesis that in more species-rich sites there could be species co-existing which have more contrasting clonal mobility than species co-existing in less species-rich sites. We also did not find any general direct relationship between species density and community clonal growth. However, we found that there are relationships that differ in different types of communities.

Decrease of species density means usually that a few species start to dominate. These species may be, although not necessarily, of certain growth forms. We have shown previously that the species that start to dominate in calcareous meadow after fertilization may belong to similar growth form with species which are lost (Sammul et al. 2003). Skipping the trees and shrubs and concentrating only on herbaceous plants the dominants are commonly either of tussock growth form, highly resistant to invasion of inhabited patch by other species (e.g. *Molina caerulea* L.), or with capability of quick clonal spread and uniform filling of the area (e.g. *Brachypodium pinnatum* L., see also Cheplick 1997, de Kroon & Bobbink 1997, Suzuki & Hutchings 1997. Herben & Hara 1997, Humphrey & Pyke 1998). Lets assume now that having high species density is the normal situation for a calcareous dry boreo-nemoral meadow. This high species density is a result of many covarying factors: low productivity, low acidity, traditional management etc. In this case both wooded meadows and open meadows have similarly low clonal mobility in the community and medium life span of ramets (Figure 3). It may be the averaging effect of having many species in the sample and thus a statistical peculiarity without any real biological explanation. Anyway, for some reasons, the species density starts to decline. This could be due to cessation of management, due to some disturbance, due to increase in productivity because of soil formation or because managers applied fertilizers, or for some other reasons. This is the situation where succession of wooded meadows and open sites, which are otherwise quite similar, goes in different directions (see also Tamm et al. 2002). In wooded meadows species with higher ramet life span and higher mobility gain in abundance. In case of abandonment the succession of these communities goes toward forests very quickly and also composition of clonal growth forms of herb-layer changes towards being more similar with forest floor community On open meadows, however, average ramet life span in community decreases, and so does also clonal mobility of the community. Such differences between different communities can not be explained as statistical artefacts anymore.

The decrease of species richness in open meadows is associated with increase in abundance of tussock species. This conclusion is supported primarily by the decreasing speed of vegetative mobility in community, but also by decreasing average ramet life span. Decrease of ramet life span in community leads to increase in speed of shoot turnover. However, it is not appointed here,

whether the ramets are replaced by conspecific ramets or by ramets of other species. We believe that the well-documented and fast turnover of shoots in species-rich communities (van der Maarel & Sykes 1993) may be as fast and as common also in species poor communities (see also Herben et al. 1994, Pärtel & Zobel 1995, Klimeš1999). It is just "hidden" behind the replacement of ramets by conspecifics which, mostly, can not be detected by counting the shoots only Many tussock-forming plants have annual ramets (e.g. *Molinia caerulea*, *Deschampsia cespitosa* L.) and thus high ramet turnover speed even inside the tussock. Still, their high capability for vegetative reproduction, small length of rhizome branches, and, hence, dense packing of ramets make them very resistant to invasions, strong patch-holders and therefore commonly dominants in undisturbed meadows. Thus, we can observe decreasing vegetative mobility and increasing shoot turnover both happening with decreasing species density in open meadows.

Contrary to suggestion that ramet turnrover may be increasing with increasing species richness are also the findings that quite often the shoots of the same species inhabit one patch for several years in species-rich communities (Klimeš 1999) and that there may be a strong positive correlation between species richness and average ramet life span in the community (Sammul et al. 2003). Our current analysis shows that there may be strong dependency of this result on type of studied community (Figure 3 A). We found that the positive partial relationship between species density and average ramet life span in the community was statistically significant only in open meadow sites. However, while there was basically no trend in this relationship in forest, the trend was marginally significant in wooded meadows, but in the opposite direction ($r_{partial}$=–0.49, p=0.0092, $p_{critical}$=0.0057), and the partial correlation coefficients were obviously different (p<0.0001). We believe the differences between communities regarding relationships between clonal growth, environment al conditions, and community structure deserve further attention.

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Table 1. General characteristics of studied sites. Aver. stands for average and St.Err. stands for respective standard error.

Site	No. of relevés	Mowing frequency (times/year)	Living biomass of ground layer (g/m^2)		Light penetration coefficient (%)		Species density ($no./m^2$)		Ramet density ($no.\times10^3/m^2$)	
			Aver.	St. Err.	Aver.	St. Err.	Aver.	St. Err.	Aver.	St. Err.
Open site 1	8	0.2	664	129	54	3.44	20	2.25	1.6	0.28
Open site 2	8	0.1	463	55	91	0.65	16	1.93	5.7	0.76
Open site 3	11	0.2	443	61	84	0.75	22	1.67	6.3	0.47
Open site 4	8	1	262	17	54	5.71	43	2.77	3.2	0.24
Wooded meadow 1	8	0.5	172	25	14	1.95	35	2.83	1.8	0.20
Wooded meadow 2	8	0.6	318	21	27	5.61	30	2.96	2.4	0.23
Wooded meadow 3	8	0.7	327	27	29	6.38	34	1.73	2.6	0.25
Wooded meadow 4	8	1	301	57	37	7.20	48	1.75	3.5	0.40
Forest site 1	8	0	99	22	3	0.66	9	0.75	0.71	0.19
Forest site 2	8	0	128	24	5	0.44	14	1.06	0.65	0.61
Forest site 3	7	0	168	22	5	1.90	13	0.59	0.59	0.89
Forest site 4	6	0	167	29	3	0.80	13	1.52	0.67	0.14
Forest site 5	8	0	93	7	5	1.19	17	1.41	0.52	0.63
Average of open sites			457	43	72	3.21	25	1.99	4.4	0.40
Average of wooded meadows			279	20	27	3.08	37	1.68	2.6	0.17
Average of forests			128	10	4	0.48	13	0.65	0.63	0.05

Table 2. Average values of community clonal growth parameters and respective standard errors (St.Err.)

Site	Ramet life span (yr)		Rhizome increment (mm/yr)		Branchng intensity (ramets /ramet year)	
	Average	St.Err.	Average	St.Err.	Average	St.Err.
Open site 1	2.06	0.10	21.5	2.9	0.53	0.06
Open site 2	1.37	0.04	8.1	0.4	0.80	0.03
Open site 3	1.58	0.04	9.6	0.4	0.83	0.03
Open site 4	2.77	0.08	29.0	6.7	0.64	0.02
Wooded meadow 1	2.92	0.16	71.1	7.1	0.54	0.03
Wooded meadow 2	3.05	0.10	81.1	5.8	0.65	0.03
Wooded meadow 3	2.42	0.10	24.0	1.9	0.67	0.04
Forest site 1	2.67	0.52	54.7	20.2	0.62	0.12
Forest site 2	3.10	0.18	63.7	7.0	0.50	0.04
Forest site 3	2.72	0.23	69.5	9.2	0.41	0.06
Forest site 4	3.93	0.39	109.1	15.5	0.40	0.05
Forest site 5	2.96	0.23	87.6	6.1	0.39	0.04
Average of open sites	1.91	0.10	16.4	2.2	0.71	0.03
Average of wooded meadow sites	2.67	0.08	51.3	5.1	0.64	0.02
Average of forest sites	3.04	0.16	75.4	6.2	0.47	0.03

Table 3. Correlation matrix of relationships between different community characteristics as estimated by Pearson correlation coefficients (r). $CV_{increment}$ is the estimate of the difference in extent of clonal mobility (coefficient of variation of rhizome increments) in coexisting species. All communities are analysed together, N=104. Statistically significant p-levels (p) are in bold script. The critical experimentwise error rate $p_{critical} = 0.0014$.

	Living biomass of ground layer		Ramet density		Species density		Mowing frequency		Light penetration coefficient		Ramet life span		Rhizome increment		Branchng intensity	
	r	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*	*r*	*p*
Ramet density	0.53	**<0.001**														
Species density	0.13	0.186	0.28	0.004												
Mowing frequency	0.12	0.221	0.26	0.008	0.88	**<0.00**										
Light penetration	0.60	**<0.001**	0.83	**<0.00**	0.23	0.017	0.19	0.052								
Ramet life span	–0.39	**<0.001**	–0.56	**<0.00**	–0.08	0.435	–0.03	0.735	–0.63	**<0.00**						
Rhizome increment	–0.47	**<0.001**	–0.66	**<0.00**	–0.40	**<0.00**	–0.37	**<0.00**	–0.69	**<0.00**	0.80	**<0.00**				
Branchng intensity	0.31	**<0.001**	0.72	**<0.00**	0.16	0.096	0.16	0.102	0.66	**<0.00**	–0.59	**<0.00**	–-0.77	**<0.00**		
$CV_{increment}$	–0.11	0.272	–0.53	**<0.00**	0.22	0.026	0.27	0.006	–0.45	**<0.00**	0.39	**<0.00**	0.24	0.013	–0.46	**<0.00**

Table 4. Type 3 effect of fixed factors of mixed model on ramet density and species density. *Habitat* is a combined factor for estimation of interactive effect of community type and mowing, *L* stands for the effect of light availability and *B* stands for the effect of biomass.

Dependent variable	Factor	N.D.f.	D.D.f.	F	p
Ramet density	habitat	6	56	9.52	<.0001
	L	7	56	8.88	<.0001
	L^2	7	56	10.46	<.0001
	B	7	56	6.23	<.0001
	B^2	7	56	4.01	0.0013
	L*B	7	56	7.84	<.0001
Species density	habitat	6	56	2.45	0.035
	L	7	56	1.97	0.076
	L^2	7	56	1.69	0.13
	B	7	56	0.58	0.76
	B^2	7	56	0.35	0.92
	L*B	7	56	1.89	0.088

Table 5. Effect of mowing, biomass and light availability on studied variables in different types of the communities. Students t-values with 56 degrees of freedom are presented with experimentwise error rate $p_{critical}$=0.05. Statistically significant t-values are in bold script. $CV_{increment}$ is the estimate of the difference in extent of clonal mobility (coefficient of variation of rhizome increments) in coexisting species.

Effect	Species density	Ramet density	Ramet life span	Rhizome increment	Branching intensity	$CV_{increment}$
Mowing on open sites	–0.4	**4.73**	–0.18	–0.08	–0.71	–0.09
Mowing on wooded meadow	0.53	1.58	0.16	0.24	0.25	–0.65
Biomass in forest	–0.65	0.24	**2.84**	**2.59**	–0.25	0.23
Biomass in open sites	1.04	**–4.08**	0.03	0.05	0.51	–0.35
Biomass in wooded meadow	–0.42	–0.74	–0.03	0.54	0.46	–0.32
Light in forest	–0.15	–0.11	–1.27	–1.19	0.2	–0.87
Light in open sites	–0.46	**4.74**	–0.17	–0.08	–0.71	–0.07
Light in wooded meadow	0.81	–0.54	0.05	–0.35	–0.31	0.09

Table 6. Pearsons partial correlation coefficients (r) between studied variables. The effect of 5 partial variables was excluded: light, biomass, their squared effects and combined effect. $CV_{increment}$ is the estimate of the difference in extent of clonal mobility (coefficient of variation of rhizome increments) in coexisting species. All communities are analysed together, N=104. Statistically significant p-levels (p) are in bold script. The critical experimentwise error rate $p_{critical} = 0.0034$.

	Ramet density		Species density		Ramet life span		Rhizome increment		Branching intensity	
	r	p	r	p	r	p	r	p	r	p
Species density	0.44	**<.0001**								
Ramet life span	–0.09	0.360	–0.04	0.690						
Rhizome increment	–0.13	0.210	–0.17	0.084	0.81	**<.0001**				
Branching intensity	0.39	**<.0001**	0.23	0.024	–0.34	**0.001**	–0.39	**<.0001**		
$CV_{increment}$	–0.26	0.010	–0.07	0.471	0.09	0.366	–0.02	0.819	–0.30	**0.002**

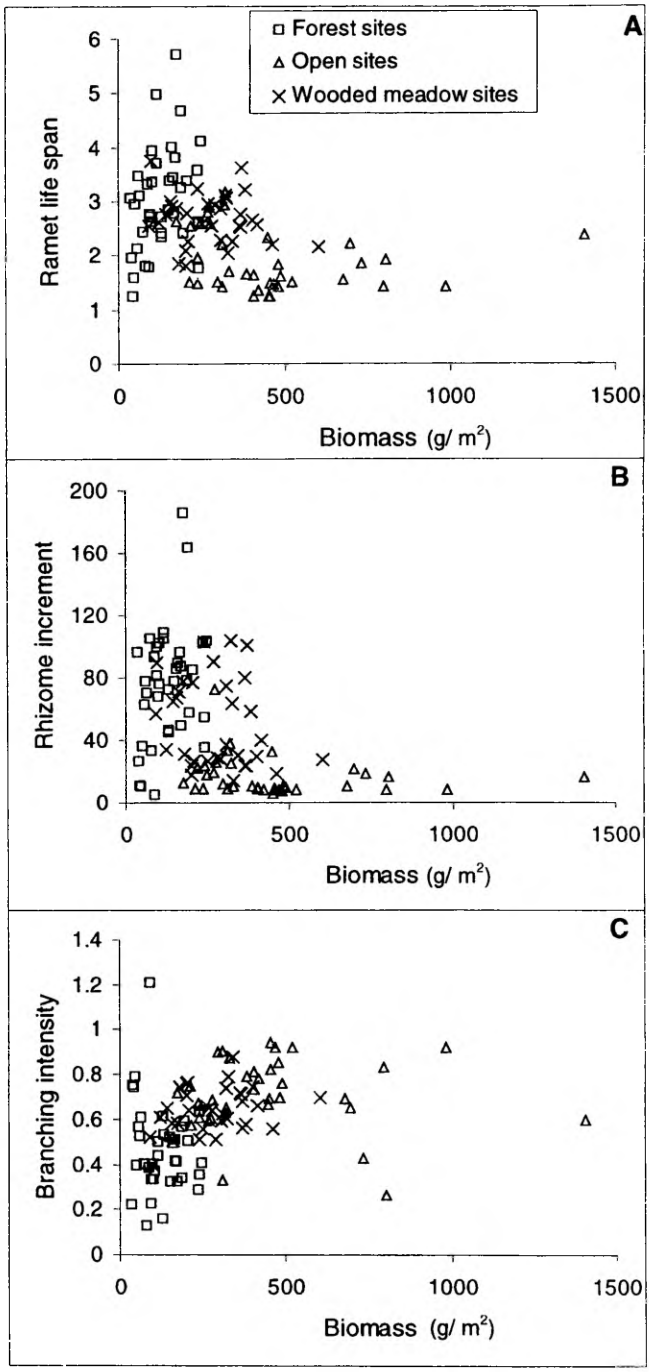

Figure 1. The average ramet life span (A), average rhizome increment (B), and average branching intensity (C) in different communities, plotted against plant living biomass of the herb layer of the community.

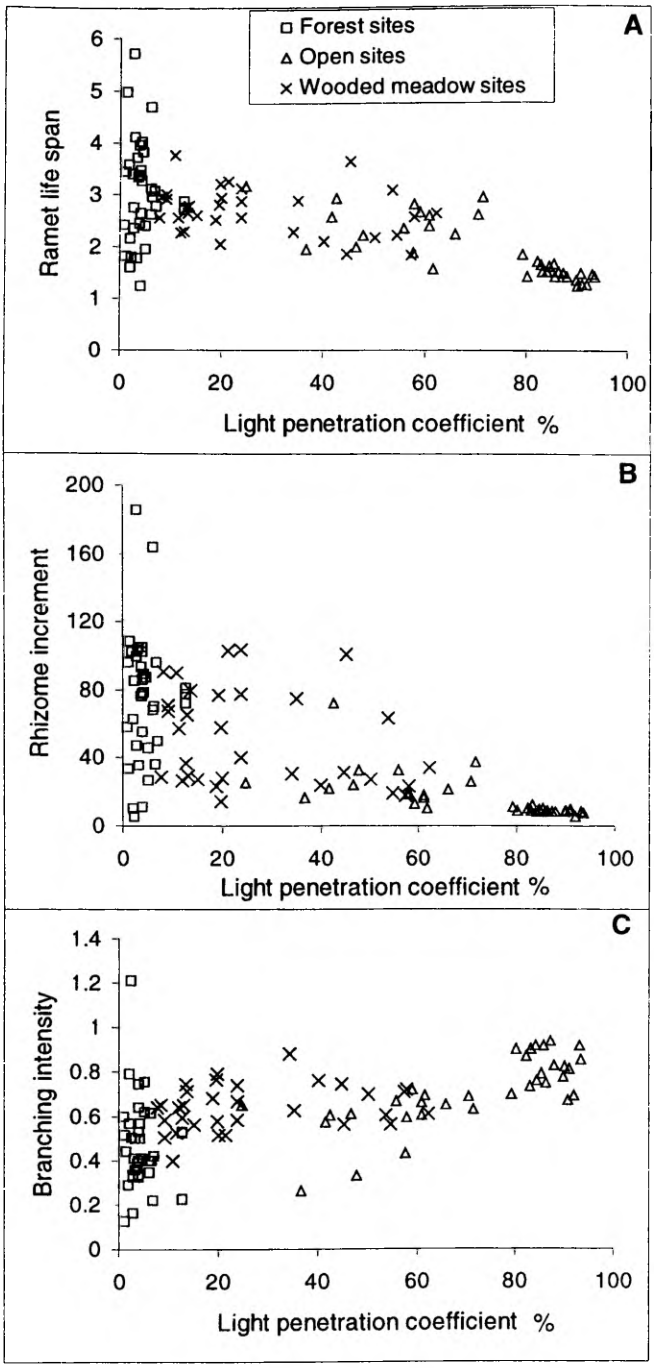

Figure 2. The average ramet life span (A), average rhizome increment (B), and average branching intensity (C) in different communities, plotted against light penetration through the tree layer.

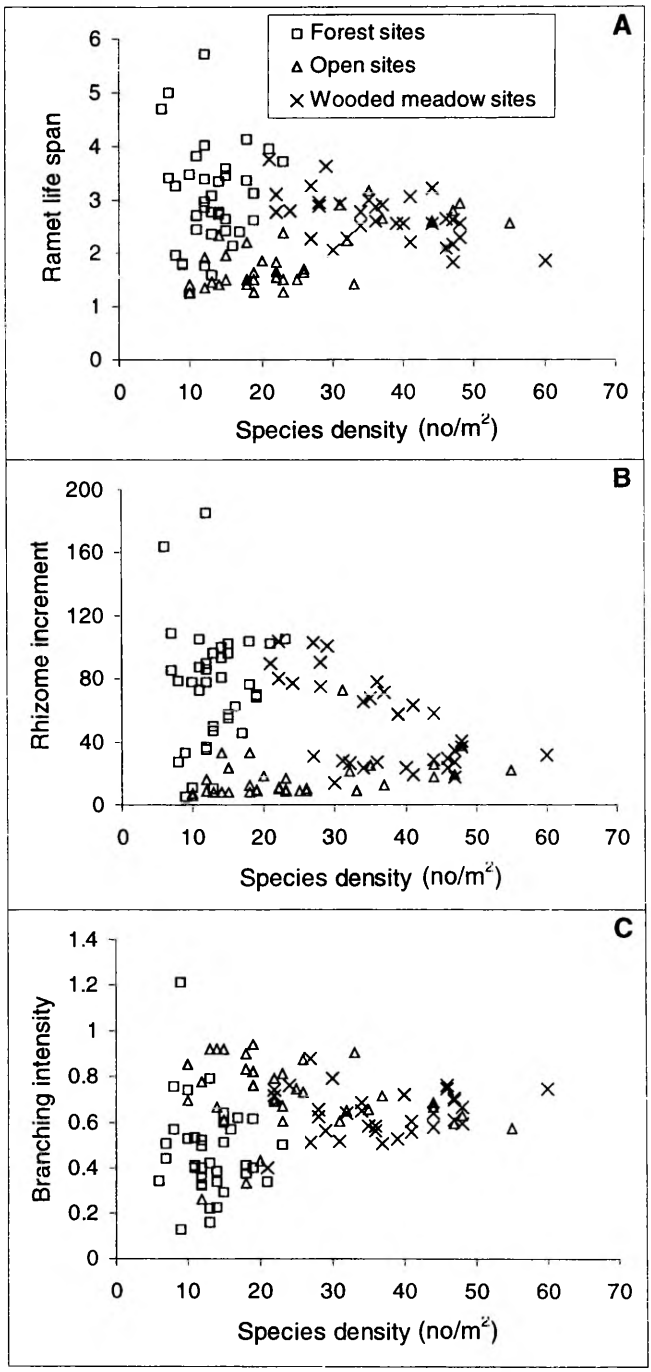

Figure 3. The average ramet life span (A), average rhizome increment (B), and average branching intensity (C) in different communities, plotted against number of vascular plant species in 1 m^2 plots.

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