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Length of the Spacer Rather than its Plasticity Relates to Species Distribution in Various Natural Habitats

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Abstract Much evidence from laboratory experiments and theoretical studies show that plasticity of clonal growth traits like lateral spread provides advantage in heterogeneous conditions. However, few tests of whether species with plastic clonal growth have an advantage over non-plastic species in natural conditions exist. I analyzed whether spacer length (i.e., length of a stolon or a rhizome branch between two ramets) and the variation of it (as a surrogate to its plasticity) relate to species presence and abundance in open meadow, wooded meadow and forest habitats with varying environmental conditions at Laelatu wooded meadow, Estonia. In fertilized, compared to unfertilized conditions, a weak and non-conclusive advantage of both long spacers and high variability of spacer length was detected. Abandonment in open meadows lead to a prevalence of species with shorter spacers, while on abandoned wooded meadows the species with longer spacers dominated. There was no difference in variability of spacer length between managed and abandoned meadows. In more heterogeneous forest habitats high variability of spacer length was more common, but the effect of lengthy spacers was more pronounced. The results suggest that while the variability of spacer length indeed corresponds with larger abundance in some conditions, the actual length of spacers has a more pronounced relationship with abundance of plants in natural vegetation.

Keywords Abandonment · Clonal plants · Fertilization · Heterogeneity · Spacer length · Wooded meadow

Introduction

The length of the spacer (either a rhizome branch or a stolon) between mother and daughter ramet (i.e., between two consecutive ramets on a rhizome or a stolon) has been a most extensively studied clonal growth trait both while evaluating

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distribution of clonal growth forms in natural habitats and while studying plastic responses of plants to changing environmental conditions. It has been shown that species with short spacers often prevail in nutrient-poor, dry and non-shaded conditions (van Groenendael et al. 1997) or other stressful habitats (Hutchings and Slade 1988; Pokarzhevskaya 1995; Kahmen and Poschlod 2008). Species with long spacers have been shown to be more common in later rather than earlier successional stages (Sammul et al. 2004; Moora et al. 2009). Plasticity of clonal growth, however, should primarily pay off in a heterogeneous environment (Hutchings and Price 1993; de Kroon and Hutchings 1995; Magyar et al. 2007) although it is crucial that the scale of heterogeneity fits the architectural constraints on degree of plastic responses of plants (Oborny 1994a; Stuefer 1996; Hutchings and Wijesinghe 1997). However, thus far the study of plasticity has rarely left laboratory or extended beyond a single-species response to environmental variation and there is no multi-species analysis of the possible implications of plasticity of clonal growth in community dynamics available (see also Zobel et al. 2010).

Response of plants to spatial heterogeneity could be divided into two phases. Firstly, plants need to be able to explore the habitat. This can better be achieved by means of long spacers, which allow a plant to reach the better microsites faster than short spacers (Slade and Hutchings 1987; Sutherland and Stillmann 1988, 1990; Cain 1994; Stuefer et al. 1994; de Kroon et al. 1996; Hutchings and Wijesinghe 1997; van Groenendael et al. 1997). Secondly, plants must be able to recognize the quality of the patch and adjust their growth in response to the environment, i.e., to display the “foraging behaviour”, prerequisite of which is the plasticity of growth (Slade and Hutchings 1987; Sutherland and Stillmann 1988; Hutchings and de Kroon 1994; Oborny 1994b). Schmitt et al. (1995) and Dudley and Schmitt (1995) argued that plasticity of spacer length is more beneficial than production of long spacers, independent of environmental conditions. However, the comparisons of benefits from long spacers and from plastic spacers are still rare, especially in natural conditions.

Suitable model systems for studying the possible relationship of clonal growth or its plasticity to community dynamics are temperate species-rich semi-natural meadows, which are strongly dominated by clonal plants (Callaghan et al. 1992; van der Valk 1992; Prach and Pyšek 1994), comprise a wide range of species, and which species composition may change rather quickly. Two main factors that cause major change in species composition of these habitats are abandonment and intensification of management (including fertilization) (e.g., Poschlod et al. 1998; Hodgson et al. 2005; Pärtel et al. 2005; Sammul et al. 2008). The main effect of fertilization on vegetation dynamics comes through an increase in competition intensity (e.g., Rajaniemi 2002). In a competitive environment long spacers could provide means for escaping competition (Bell 1984; Schmid and Harper 1985; Svensson and Callaghan 1988; Herben et al. 1994) while species with short spacers, which lead to clumped growth, may be competitively superior (Gough et al. 2002). It has also been shown that competition may lead to an increase of the spacer length in stoloniferous plants (Schmid 1986; Price and Hutchings 1996; van Kleunen and Fischer 2001) and to a decrease in a rhizomatous plant (Cheplick 1997), thus suggesting a plastic reaction of plants to the competition. Increase in nutrient availability has been shown to enhance a plant’s ability for plastic responses (e.g., Huber et al. 1998; Stoll et al. 1998; Kleijn and van Groenendael 1999). Hence, even though most studies report increase of abundance of species with longer spacers in response to increasing productivity and competition intensity (e.g., Song et al. 2002; Sammul et al. 2003) the results remain contradictory.

There is also much confusion about whether spacer length contributes to a species ability to withstand effects of abandonment of grassland management (see also Klimešová et al. 2008). Kahmen and Poschlod (2008) have shown that grassland management favors perennial plants with clonal growth, but there is no advantage in having either long or short spacers. Kahmen et al. (2002) and Klimešová et al. (2008) showed that there is less lateral spread in clonal plants in managed compared to abandoned meadows. Römermann et al. (2009), on the contrary, found an increase of species with long spacers in mown meadows and a decrease in average lateral spread of species of abandoned meadows. I am not aware of any comparison of plasticity of spacers and the effect of grassland abandonment.

The main aim of this study is to compare the advantage of plasticity of spacer length to the possible advantage of having either short or long spacers in various natural habitats: *i*) in fertilized meadows (increased productivity and competition intensity); *ii*) in communities with different levels of environmental heterogeneity; and *iii*) in abandoned meadows. I use the data on variation of spacer length of the 106 most common species from Laelatu wooded meadow and treat them as an approximation of a plant's capability for plastic responses to environmental variation. Even though such an approach is not a direct estimation of a plant's reaction norm with regard to a specific environmental factor (as suggested by e.g., Thomas and Bazzaz 1993 and de Kroon et al. 2005), the variation of clonal growth parameters of plants sampled from different parts of a rather variable habitat (see below) can still be treated as a first step towards comparative analysis of advantage of plasticity in natural plant communities. The quantitative database of clonal growth of meadow plants (Tamm et al. 2002; Sammul et al. 2003) allows the simultaneous assessment of whether species with different spacer length or with different variability of spacer length prevail in different communities. A long-term fertilization experiment carried out at Laelatu (Pork 1969; Sammul et al. 2003) provides data on the effects of increased fertility of the site and consequently increased competition intensity on species composition. The varying history and management regimes of different parts of Laelatu provides further information for comparisons of the effects of abandonment and heterogeneity of environmental conditions on species composition. To separate the effect of abundance of a species from mere presence of a species in the community I will compare average value of spacer length to abundance-weighted average of spacer length.

Methods

Study Area

The 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. The total area of the meadow is about 100 ha and it has been exploited for hay cutting for at least 300 years, but today only 15 ha at most are mown regularly (Kukk and Kull 1997). 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. Mean temperature for July is 17°C and for January -5°C. Annual mean temperature is 6.3°C. Mean annual precipitation is 500–600 mm, the most rainy season is autumn.

The vegetation of the Laelatu wooded meadow is characterized by a very high richness and species density. The maximum number of vascular plants in a 20×20 cm plot is 42 and in a 1 × 1 m plot 76 (Kull and Zobel 1991; Kukk and Kull 1997; Sammul et al. 2008). The flora of vascular plants in the Laelatu wooded meadow and in adjacent areas comprises 470 species, while 225 species are known directly from the wooded meadow (Kukk and Kull 1997). The vegetation belongs mostly to the *Sesleria coerulea-Filipendula hexapetala* association (Krall and Pork 1970). The tree layer covers (crown projections) on average 30%–50% of the ground surface and consists of *Quercus robur* L., *Betula* L. spp., *Fraxinus excelsior* L., *Populus tremula* L., etc. (Kukk and Kull 1997). The abandoned parts of the wooded meadow are nowadays covered with deciduous forests of different age. The dominant tree species in the forests are *Betula* spp., *Fraxinus excelsior*, *Populus tremula* and *Alnus incana* (L.) Moench.

Environmental conditions in studied forests and wooded meadows vary more than conditions on open meadow sites (Table 1). Most variables vary most in forests, but vegetation density and light penetration through the tree layer are most variable in wooded meadow sites. Only the number of species per 1 m^2 is more variable in open meadow sites than in wooded meadows. The highest variation in species richness is again found in forest sites.

Clonal Growth Traits

The clonal fragments of the 120 most abundant species of the Laelatu wooded meadow were excavated between 1988 and 1997 to measure clonal growth parameters. Most excavations took place in 1995–1996. For each species at least

Table 1 Basic vegetation characteristics of forests, wooded meadows and open meadows describing heterogeneity of the conditions in each habitat as estimated by a coefficient of variation (Coeff. Var.). Larger value of a coefficient of variation indicates larger variability of a respective trait and, thus, larger heterogeneity of respective conditions

Characteristics	Forest		Wooded meadow		Open meadow	
	Average	Coeff. Var.	Average	Coeff. Var.	Average	Coeff. Var.
Number of species (/m^2)	14	0.27	53	0.13	44	0.17
Total cover of vascular plants (%)	49	0.30	71	0.16	80	0.08
Total cover of mosses (%)	14	0.27	44	0.18	53	0.13
Plant biomass (g/m^2)	42	0.49	116	0.40	217	0.30
Shoot density (nr/m^2)	209	0.51	16431	0.541	4287	0.27
Light availability to ground layer (%)	4.48	0.66	24.7	1.10	88	0.097

10 clonal fragments with about 50–100 ramets in total were collected from different parts of the wooded meadow (varying in light availability, soil moisture, mowing frequency, productivity, etc.), to cover most of within-species variation and a large range of ecological conditions in which plants grow. Based on the scars from the dead shoots on the rhizomes as well as the size and morphology of the internodes and nodes on the rhizomes, ramet age was estimated, the annual increment of the clonal spacers was measured, and the number of the clonal offspring per ramet was counted (as described in detail in Tamm et al. 2002; Sammul et al. 2003, 2004). In the current study only the data about the length of annual increment of rhizomes and other spacers are used.

For all other means of vegetative reproduction, besides rhizomes (bulbils, stolons, shoots from root buds), the distance between two consecutive shoots on a rhizome branch or a stolon (i.e., between "mother" and "daughter" ramets), which in most cases is the distance between the shoot of the previous year and the one of the current year, was estimated and is referred to here as spacer length. The only species with regular resprouting from roots in the set of species studied was *Ophioglossum vulgatum* L., for which the length of the root part from the "mother" ramet to the "daughter" shoots sprouting from root buds was measured and treated as a measure of spacer length. As an approximation of potential for spacer length plasticity the variation of spacer length is used, which is estimated by coefficient of variation. The main advantage of coefficient of variation over other measures of variability is that it enables avoidance of co-variation between length of the spacers and variation of spacer length, which is crucial in the current study where the two measures are going to be compared to each other.

For 42 species out of 148 found in the vegetation samples, it was either impossible to measure the length of clonal spacer, or the sample size was very small (<5). However, such species occurred with very low frequency and small abundance in the vegetation descriptions, hence their impact on results is small.

Fertilization Experiment

In 1961, a fertilization experiment was set up by K. Pork in the most regularly mown, uniform, open, mesic, and old part of the Laelatu wooded meadow (Pork 1969). Twelve 10 × 30 m permanent plots were marked and randomly assigned to four treatments (non-fertilized control and three treatments with increasing amount of fertilizers) with three randomized replications. This study only compares a control to the treatment that received the highest quantity of fertilizers – 2.6 g/m^2 of phosphorus, 5 g/m^2 of potassium and 10 g/m^2 of nitrogen annually in the form of potassium phosphate and ammonium nitrate. Fertilization lasted from 1961–1981 and vegetation recovery after cessation of fertilization has been monitored since 1985. This study uses the data from the end of the fertilization period, by which the average dry weight of the above-ground plant biomass was 129 g/m^2±11 (standard deviation) in control and 384 g/m^2±51 in fertilized treatment (Sammul et al. 2003). The plots were mown every year at the beginning of July and hay was removed.

To sample vegetation composition all plants from approximately 20 randomly located small areas (approx. 150 cm^2) were cut close to the ground (see Sammul et al. 2003 for more details). Plot edges were avoided, the buffer zone was approximately 1–1.5 m wide. All small samples were pooled and plant parts were thereafter sorted according to species, dried and weighed. Litter and more than one-year-old parts of plants were excluded from biomass samples to only account for annual biomass production. The relative proportion in weight was calculated for each species and used as an estimate of relative abundance.

For the current study the last five years (1977–1981) of the fertilization period were utilized to reduce the effect of between-year variation in species abundance. An average relative abundance (share in biomass) of each species over three plots during five years (three replicates per each treatment) was calculated and used in further data analysis.

Areas with Different Environmental Conditions and Mowing Regimes

A total of 123 vegetation analyses available from earlier studies (Sammul et al. 2004; Otsus et al., unpubl. data) were used for comparison of areas with different environmental conditions. 1 m^2 study plots were located at 11 different sites: four sites of deciduous forest (37 relevés), four sites of wooded meadow (28 relevés) and three sites of open (devoid of trees) calcareous meadow (15 relevés). Next to the most well-managed wooded meadow (two sites with 15 relevés) and all open meadow sites were relatively similar, but abandoned (unmown for at least 10 years) sites and their vegetation described using 24 and 19 relevés respectively. In each plot, all vascular plant species were recorded and their cover was estimated. The average cover of each species in different groups of sites was calculated and used in further data analysis.

Data Analysis

For each plot the average value of length of spacer and of coefficient of variation of spacer length of species found in that plot was calculated. These averages consider only presence of species and ignore their abundance. To take into account also relative abundance of species, the weighted average of spacer length in each plot was calculated as follows (see also Sammul et al. 2003, 2004; Moora et al. 2009).

$$L = \sum a_i l_i / \sum a_i$$

Here L denotes the weighted average of spacer length, a_i is the relative abundance of species i in the plot and l_i is the spacer length for species i. Weighted average takes into account the differences in species abundances between different plots so that abundant species have more impact on average and the impact of rare species (such as solitary individuals occurring on the plot due to random events) is diminished. Unweighted average only accounts for species presence on the plot and both rare species and abundant species contribute equally to the average. Thus, while the latter describes what kind of species inhabit the plot, the former more precisely describes the actual structure of the vegetation.

Differences in average values of length of spacer, coefficient of variation of spacer length and abundance-weighted average of spacer length between *i*) fertilized and non-fertilized plots; *ii*) open meadow, wooded meadow and forest plots; and *iii*) abandoned and mown plots in open meadows and wooded meadows were tested using type III one-way analysis of variance. Tukey HSD test was used for detection of homogeneous groups.

To estimate whether species with longer spacer or with larger variation of spacer length were more abundant in a particular habitat a linear correlation (Pearson r) between coefficient of variation of spacer length of a species and the average abundance of a species in particular type of meadow was estimated. For better fit with normal distribution, length of spacer was log transformed and species abundance was log(x+1) transformed prior to the correlation analysis. Casewise deletion of missing data was used in those circumstances when the database did not enable estimation of variation of spacer length of a species. All statistical tests were applied using the program Statistica 8 (StatSoft, Inc. 2008).

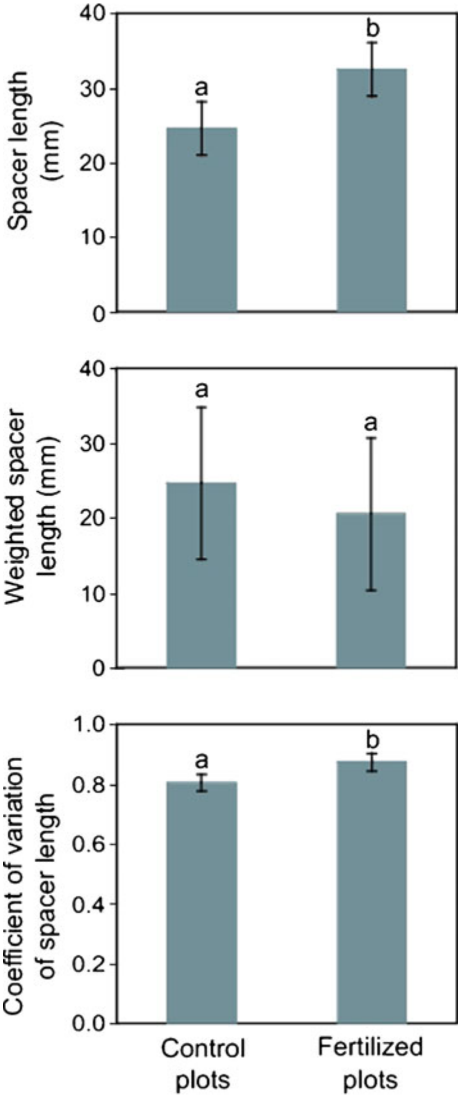
Results

The vegetation of fertilized plots on average consisted of species with longer spacers compared to non-fertilized plots ($F_{1,\ 4}=18.6$, $P=0.012$), but when species abundance was taken into account in calculation of weighted average of spacer lengths, there was no difference between fertilized and non-fertilized plots ($F_{1,\ 4}=0.63$; Fig. 1). Vegetation of fertilized plots also consisted of species with larger variation in spacer lengths ($F_{1,\ 4}=22.5$, $P<0.01$). There was no correlation between relative abundance of a species and either spacer length or variation of spacer length in non-fertilized plots while there was a weak positive correlation between variation in spacer length of a species and relative abundance of a species in fertilized plots (Fig. 2).

The vegetation of forest sites consisted on average of species with longer spacers than the vegetation of wooded meadows or open meadows ($F_{2,\ 77}=84$, $P<0.0001$; Fig. 3). This difference also persisted when clonal mobility was estimated using abundance-weighted average of spacer length ($F_{2,\ 77}=67$, $P<0.0001$). On average, vegetation of forest sites also consisted of species with larger variation of spacer length than vegetation of wooded meadows or open meadows ($F_{2,\ 77}=31.5$, $P<0.0001$). There was a positive correlation between the spacer length and species abundance in forests (Fig. 4). There was no correlation between variation of spacer length and species abundance in any of the studied habitat types.

In abandoned open meadows compared to mown meadows, species with shorter spacers dominated (Fig. 5). This result was the same regardless of whether only averages of spacer lengths were compared ($F_{1,\ 32}=37.2$, $P<0.0001$) or whether species relative abundances were also taken into account ($F_{1,\ 32}=10$, $P<0.005$). On wooded meadows the results were exactly the opposite: species with longer spacers prevailed in abandoned sites (for average spacer length $F_{1,\ 37}=13.8$, $P<0.001$; for abundance-weighted average spacer length $F_{1,\ 37}=31.2$, $P<0.0001$). No difference in relative abundance of species with different variability of spacer length was found either between managed and abandoned wooded meadows or open meadows (in both cases $F<2$, $P>0.2$). Species abundance in abandoned wooded meadows was positively correlated to its spacer length (Fig. 6). Neither the same relationship in open meadows nor the correlation between abundance and coefficient of variation of spacer length of a species were statistically significant.

Fig. 1 Average spacer length values of whole vegetation in fertilization experiment. Bars denote 95% confidence intervals of a mean. Letters above columns mark homogeneous groups according to Tukey HSD test ($P<0.05$). N=3 for both groups



Discussion

In this study three different comparisons between the community-wide distribution of species with different length of the spacer and with different plasticity of the spacer length were made based on differences in plants environment: increase in productivity and consequent competitive intensity (fertilization experiment), increase in heterogeneity of the environment (comparison between open and wooded meadows, and their comparison to forests), and the effect of meadow abandonment. Previous studies have suggested that after any of these environmental changes species with either long spacers or large variation of spacer length should get an

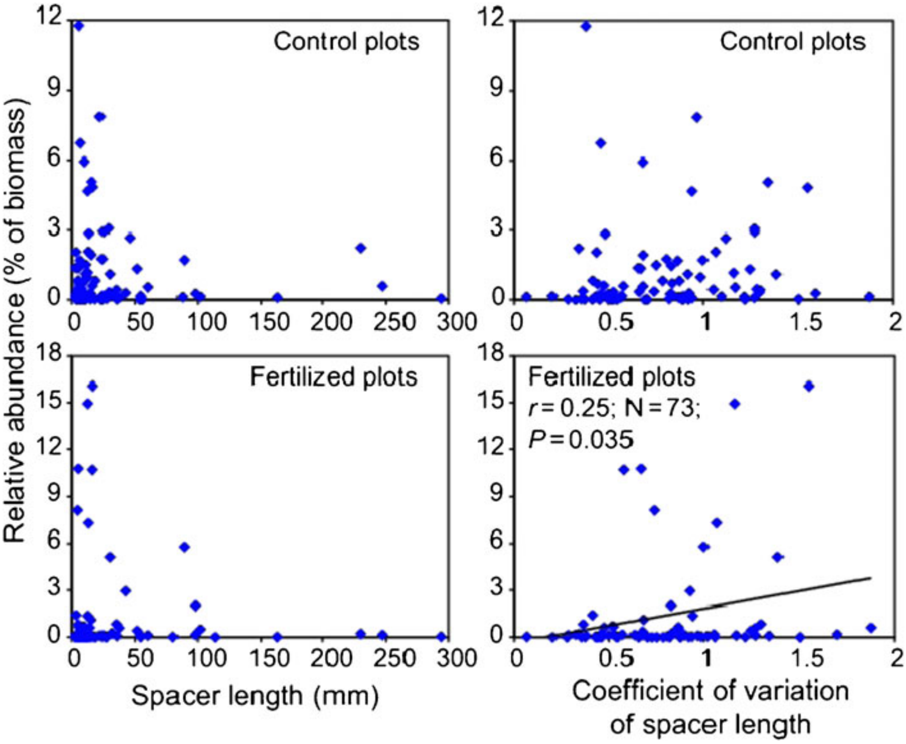


Fig. 2 Correlations (*r* – Pearson correlation coefficient) between relative abundance of a species and its spacer length or its coefficient of variation of spacer length in the fertilization experiment. A trendline is plotted only in the case of a statistically significant ($P<0.05$) correlation. N – sample size

advantage, but these predictions have not always been confirmed. Current results only partially support the original hypotheses.

It appears that the vegetation in fertilized areas includes more species with long spacers than vegetation of non-fertilized areas (Fig. 1), which matches some earlier observations (de Kroon and Schieving 1990; van Groenendael et al. 1997; Humphrey and Pyke 1998; Song et al. 2002). However, there was no tendency for species with longer spacers to dominate in fertilized areas. It is hard to decouple the effects of competition and productivity in natural fertilization experiments where the scope is vegetation change even though both usually increase with fertilization (e.g., Grime 1979; Rajaniemi 2002; Suding et al. 2005). Shorter spacers may be advantageous in competition as they lead to more compact placement of ramets and strong tussocks, which are hard for other species to invade and are competitively superior (Winkler and Schmid 1996; Herben et al. 1997). Shorter spacers also enable stronger physiological integration between ramets, and this has been proposed as the main process that provides an advantage to clonal plants in competition (Suzuki and Hutchings 1997, but see Peltzer 2002). Longer spacers, however, may provide an advantage for a competitively inferior species to avoid competitive interactions by “running away” (Schmid and Harper 1985; Huckle et al. 2000). Combining these two predictions, one might expect an increase in variability of clonal mobility or in difference between longest and shortest spacers in fertilized habitats. This could

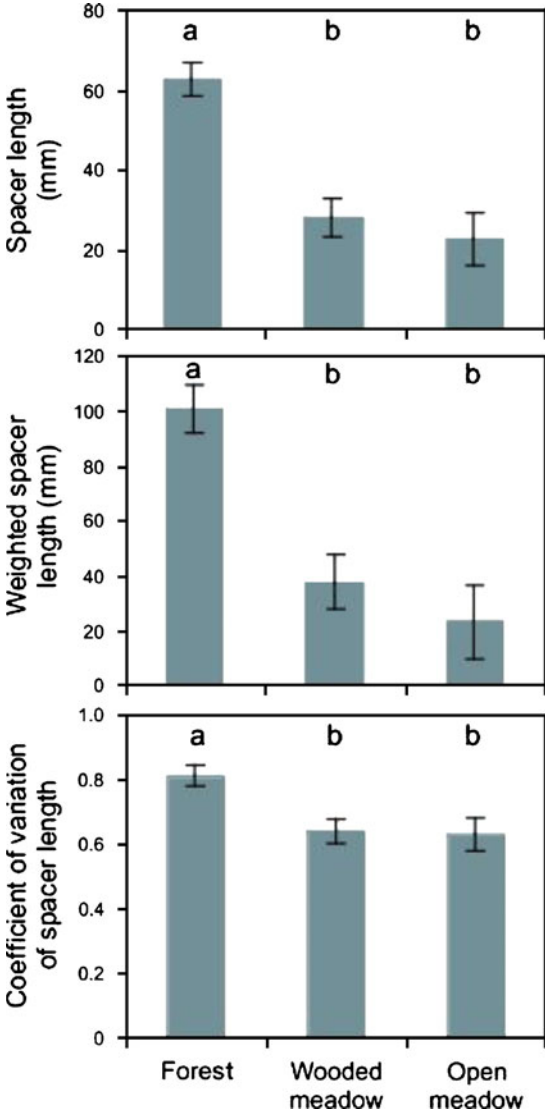


Fig. 3 Comparison of average spacer length values of whole vegetation between forests (N=37), wooded meadows (N=28) and open meadows (N=15). Bars denote 95% confidence intervals of a mean. Letters above column mark homogeneous groups according to Tukey HSD test (*P*<0.05)

strongly influence species coexistence (e.g., Moora et al. 2009), however, no indications for such changes could be detected in the current data (see also Sammul et al. 2004).

Vegetation in fertilized plots also had relatively more species with higher variation of spacer length than vegetation in non-fertilized control plots (Figs. 1 and 2). The effect of overall level of productivity on plasticity of species has rarely been addressed (but see Stoll et al. 1998; Kleijn and van Groenendael 1999). Huber et al. (1998) demonstrated that when nutrients are limiting an optimal distance between ramets may exist, in which case plasticity of spacer length is not advantageous. Kleijn and van Groenendael (1999) showed that in a more productive environment plant response to a suitable patch is stronger than in less productive conditions. Increasing productivity may allow more extensive growth responses of plants

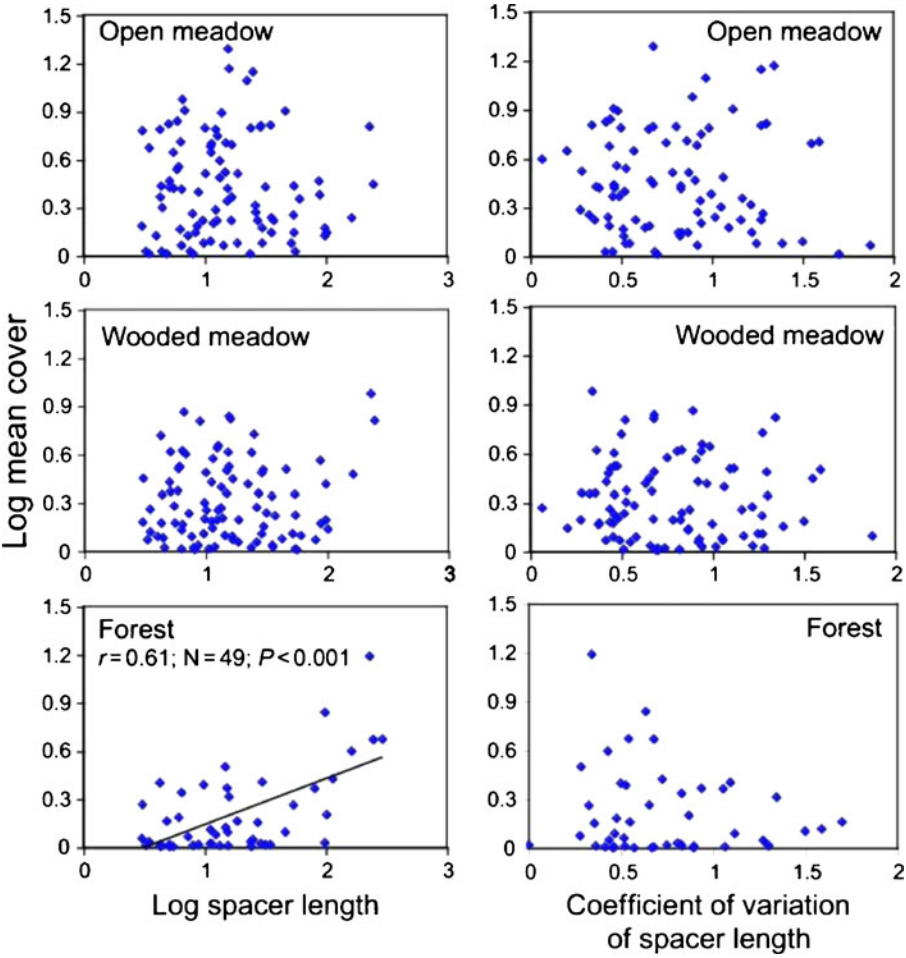
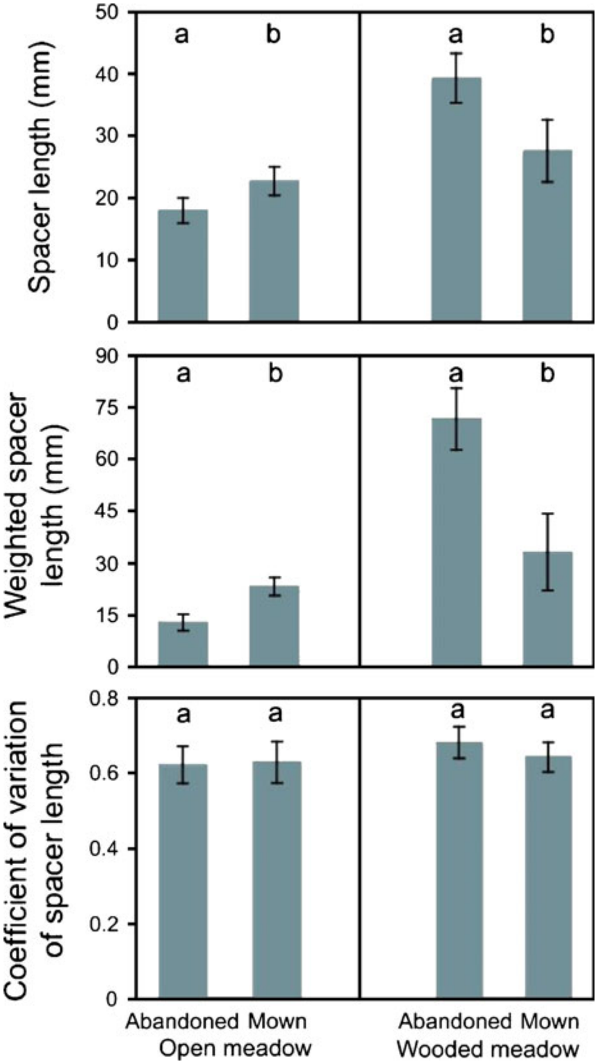


Fig. 4 Correlations between average abundance of a species and its spacer length or its coefficient of variation of spacer length in studied forests, wooded meadows and open meadows. A trendline is plotted only in the case of a statistically significant correlation. Abbreviations as in Fig. 2

(Grime et al. 1986; Crick and Grime 1987; Dong et al. 1996) thus enabling plastic responses of plants or just enabling larger growth. Some species clearly change (usually increase) the length of their spacers in response to fertilization (e.g., Dong et al. 1996; Stoll et al. 1998), suggesting the benefit of plasticity. However, it is difficult to conclude yet, whether the observed patterns describe just the growth responses of plants to increased resource availability, or a special adaptation to nutrient-rich and competitive environment (see also van Kleunen and Fischer 2001). Moreover, it has also been suggested that high rates of resource exploitation in more productive conditions create localized zones of depletion (Crick and Grime 1987; Callaway et al. 2003). Thus, plants may react to heterogeneity along with nutrient availability.

The success of a plant in heterogeneous conditions depends on the scale at which the heterogeneity appears in nature and whether it is within a plant's reaction norm (Oborny 1994b; Stuefer 1996; de Kroon et al. 2005). The current study did not explicitly measure the nature or scale of heterogeneity in the evaluated study

Fig. 5 Comparison of average spacer length values between mown and abandoned wooded meadow (N=15 and 24 respectively) and open meadow sites (mown areas – N=15; abandoned areas – N=19). Bars denote 95% confidence intervals of a mean. Letters above columns mark homogeneous groups within a habitat type according to Tukey HSD test ($P<0.05$)



systems. Instead, it relies on the assumption that variability detected between sample plots indicates a general heterogeneity of the habitat (Table 1; see also Downing 1991). As vague as this approximation is, it still provides a first insight into the possible correspondence between variability of the habitat and the relative advantage this provides for more plastic species. On average, vegetation of forest sites consisted of species with larger variation of spacer length, thus confirming that plants with greater plasticity could have an advantage in more heterogeneous environments (Bradshaw 1965; Donohue et al. 2000). However, the difference between forests and meadows in the average length of the spacer was even larger (Fig. 3) and the abundance of species was positively correlated with spacer length, but not with its variability in forest habitats (Fig. 4). This suggests that the length of the spacer might be even more important than mere plasticity of spacer length in

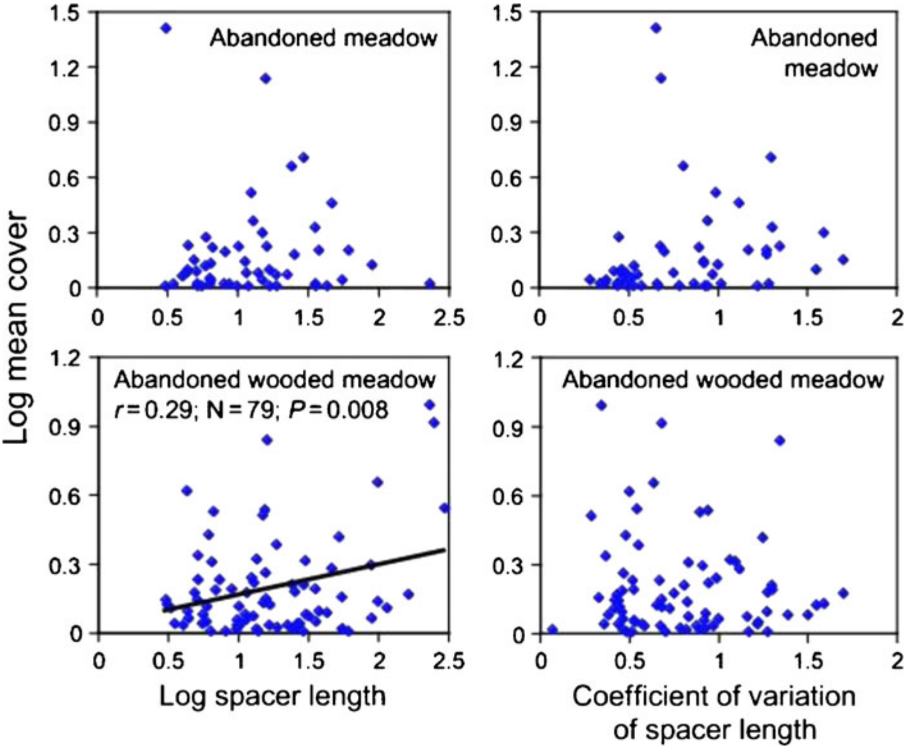


Fig. 6 Correlations between average abundance of a species and its spacer length or its coefficient of variation of spacer length in abandoned wooded meadow and open meadow sites. A trendline is plotted only in the case of a statistically significant correlation. Abbreviations as in Fig. 2

heterogeneous natural habitats. Longer spacers allow for the exploitation of patchily distributed resources, and enable a plant to reach suitable microsites faster than shorter spacers (Sammul et al. 2004; Wildová et al. 2007). Hence, their prevalence in more heterogeneous sites is to be expected. However, the very coarse approach used here does not allow firm generalizations and the comparison of positive effects of plasticity and spacer length in exploration of heterogeneous natural systems needs to be more thoroughly analyzed in further studies.

Earlier results on the changing balance between species with different clonal mobility after abandonment of meadow management have been contradictory (Kahmen et al. 2002; Tamm et al. 2002; Kahmen and Poschlod 2008; Klimešová et al. 2008; Römermann et al. 2009). While this study found no change in average variability of spacer length after abandonment, there was a change in average spacer length following abandonment and it differed between open meadows compared to wooded meadows. On abandoned open meadows, species had, on average, shorter spacers than species on mown sites. On wooded meadows, abandonment led to an increase of species with longer spacers. It has been shown before that transition dynamics of community-wide distribution of clonal growth traits on open meadows and wooded meadows could be different (Sammul et al. 2004). The latter quickly transform to forests, while on open meadows, species first have to cope with increased competitive interactions. The fertilization experiment (see above) also indicated that short spacers could be advantageous in competition, thus providing some corroborative evidence. However, there is very little information yet on how clonal growth influences species interactions during successional changes. Given that clonal growth is very likely to contribute to the delay of extirpation of populations during habitat loss (Eriksson and Ehrlén 2001; Colling et al. 2002; Brys et al. 2003) current results point towards an important mechanism in vegetation development that could have implications for nature conservation.

The value of plasticity lies in the ability of a plant to respond to a changing environment (Hutchings and de Kroon 1994; Alpert and Stuefer 1997; de Kroon et al. 2005). Even though this study did not directly address the plasticity of clonal expansion, the variation of spacer length provides a good approximation of a plant's capability for plastic response to spatial heterogeneity. There is very little information yet on the importance of plasticity of clonal growth in natural conditions. Plasticity is of course a new trait in comparative analyses of vegetation dynamics and it is not yet included in databases of clonal growth types of plants (e.g., CLO-PLA – Klimeš and Klimešová 1999; Klimešová and Klimeš 2006; LEDA – Kleyer et al. 2008). However, most studies of functional vegetation analyses ignore clonal growth traits in general even though the accumulation of information regarding clonal growth and the variability of it as well as about factors influencing that variability enables the community-wide analyses of clonal growth of plants. The extrapolation from within-species plastic growth responses to interspecific advantages in community dynamics is not simple because differences between species in habitat preferences, growth rate, competitive ability etc. need to be tackled. However, this transition is badly needed to advance the study of plasticity of clonal growth and to fully understand the role of environmental heterogeneity in population and community dynamics. The results of the current research demonstrate that advantages of plasticity of clonal mobility can indeed be detected at the community level, especially in heterogeneous habitats. However, the actual length of spacers seems even more important.

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