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# Small-scale plant mobility in a species-rich grassland

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**Abstract.** Plant mobility was studied in a species-rich grassland in S. Moravia (Czech Republic) at scales from 0.0025 to 2.25 m$^2$. Cumulative species numbers, cumulative species frequencies and the distribution of distances between sites of occurrence in particular years were established using data collected from 1991 to 1997. The observed values were compared with null models of completely random and restricted random movement of the plants. Most plants persisted at a spot more frequently than expected from the completely random model and with a few exceptions they also spread to neighbouring subplots more often than expected. Cumulative species numbers were between the ranges predicted by the two random models and increased linearly during the 7-yr period at all scales, indicating a large species pool. The role of clonal spreading and of generative reproduction depended on the growth form of the species. I conclude that a high species richness is not necessarily linked with a high plant mobility, even if coexistence of plant species may be promoted by plant mobility.

**Keywords:** Cumulative species number; Cumulative species frequency; Grassland diversity; Plant mobility; Randomization; Scale-dependence.

**Nomenclature:** Ehrendorfer (1973).

## Introduction

At small spatial scales grasslands belong to the most species-rich plant communities in the world. For example, 42 species have been recorded on 20 cm × 20 cm and up to 63 species on 1 m$^2$ in Estonian wooded meadows (Kull & Zobel 1991). Numerous mechanisms have been suggested to explain how such high species numbers can be maintained (e.g. Wilson 1990; Huston 1994; Palmer 1994). Not all of them are, however, sufficient to explain coexistence in dry grasslands where the highest values of species richness have been found. The role of interspecific competition is usually crucial in explanations of mechanisms of species coexistence in non-disturbed plant communities, because species decline is mostly caused by competitive exclusion (Ricklefs & Schluter 1993; Palmer 1994; Rosenzweig 1995). It has been suggested that species mobility is a mechanism which may suppress the effect of competitive exclusion (Bell 1984; Caswell & Cohen 1991; Herben et al. 1997). Plants moving around change neighbours and therefore suffer from competition once more, the next time less than their neighbours due to the differences in competitive ability of individual plants. If the inferior competitor is moreover more mobile than the superior one, the effect of competition may be balanced at the community level and competitive exclusion is postponed. If this mechanism is effective then the greater the differences in competitive effects caused by individual species are, the higher the difference in mobility of strong and weak competitors required to prevent species reduction will be.

Our knowledge of plant mobility in grasslands is based on some detailed studies of several m$^2$ in a few sites in the world (van der Maarel 1996 and references therein; Geißelbrecht-Taferner et al. 1997). So far, open plant communities with sparse cover, grazed or abandoned and irregularly disturbed by climatic extremes have been studied. In other types of plant communities plant mobility of all present species has been studied rarely (but see Maubon et al. 1995; Økland 1995). Plant mobility in grasslands has been inferred from year-to-year changes in species composition (Glenn & Collins 1990, 1993; Stampfli 1995; Hobbs & Mooney 1995; Zhang & Skarpe 1995) from cumulative species numbers and from cumulative species frequency (van der Maarel & Sykes 1993, 1997; Sykes et al. 1994; Pärtel & Zobel 1995; van der Maarel et al. 1995; van der Maarel 1996; Geißelbrecht-Taferner et al. 1997) and from persistence of species in particular subplots (Herben et al. 1993, 1997). The results indicate that plant mobility increases with decreasing scale (Sykes et al. 1994; van der Maarel & Sykes 1997) and is particularly high in dry open grasslands where most species are short-lived (van der Maarel 1996). The small size of individual plants and their high density in early successional stages is another factor causing high plant mobility (Pärtel & Zobel 1995). It has also been assumed that disturbance, such as recurrent drought, may enhance plant mobility (van der Maarel 1996). Growth form may determine plant mobility to a large extent (Herben et al. 1993). However, the positive effect of plant mobility on species coexistence predicted in several theoretical studies (Bell 1984; Caswell & Cohen 1991) is still uncertain (Herben et al. 1997). Besides, there are some other related topics which have been rarely studied, such as spatial aspects of plant mobility.

Here, I present an analysis of plant mobility in a plant community which is closed, with no real gaps and no external disturbance caused by grazing, rodents, fire, droughts or humans, except regular mowing once a year. Species richness is remarkably high in this grassland and annuals are scarce. In particular the following questions were addressed: 1. To which extent is spreading of plants over different distances a random process? 2. How is plant mobility cumulated over time? 3. How is plant mobility related to growth form?

## Study area

I established a permanent plot in the Bílé Karpaty Mountains, Czech Republic (48° 54' N, 17° 25' E). Mean monthly temperatures were 9.4 °C and the mean annual precipitation was 464.1 mm over the last 10 yr (data from the Meteorological station at Strážnice, 8 km from the plot). The plot is situated in a grassland with scattered *Quercus robur* trees, in the National Nature Reserve of Čertoryje, at an altitude of 440 m a. s. l. The grassland area is situated on a SW-facing slope with an inclination of 5 to 10 °. Soil conditions are as follows:

pH [$H_2O$]: 5.99 Total nitrogen: 0.47 % Total carbon: 5.45 %
Ca: 8.42 mg/g K: 0.05 mg/g Mg: 0.72 mg/g
Na: 0.052 mg/g P: 0.234 mg/g*
*estimated in a 1M $BaCl_2$ extract, with the ICP OES method.

The grassland has not been fertilized in recent decades. It is dominated by *Bromus erectus*. Other important species are *Carex montana, Potentilla alba, Molinia arundinacea, Carex caryophyllea* and *Festuca rupicola*. Maximum above-ground biomass ranged from 247 to 412 g/m$^2$ from 1989 to 1997 – mean value 335 g/m$^2$. The proportion of dicotyledonous plants in the above-ground biomass is ca. 40% (Klimeš unpubl.). A more detailed description of the species composition of the plot and the environment is given in Jongepierová et al. (1994) and Klimeš et al. (1995).

The permanent plot is 1.5 m × 1.5 m in size; it was established in 1991. It was divided by cord into 900 subplots of 5 cm × 5 cm. In these subplots, presence/absence of rooted vascular plants was recorded during the second week of June, from 1991 to 1997, usually 1 to 3 weeks before the meadow was cut. For details on species richness and the number of individuals see Klimeš (1995).

The vascular plants were arranged in four groups, further called growth forms, according to their potential mobility resulting from their morphology (Fig. 1). The classification of plants is based on the database CLO-PLA1; see Klimeš et al. (1997) and http://www.butbn.cas.cz/klimes for details.

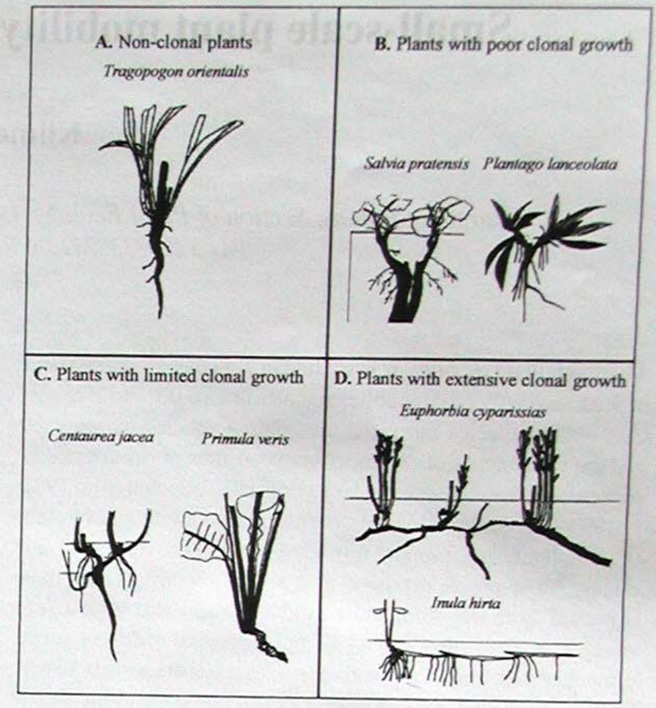

**Fig. 1.** The four growth forms distinguished in this study.
A: Annuals, biennials and short-lived perennials without clonal growth;
B: Perennials with limited clonal spread; their tap root may decay from its centre in senescing plants, causing plant fragmentation resulting in small-distance spread.
C: Perennials with short rhizomes which may grow ≤ 5 cm/yr;
D: Perennials with long rhizomes growing > 5 cm/yr, with either root-derived (e.g. *Euphorbia cyparissias*) or stem-derived (e.g. *Inula hirta*) organs of clonal growth.

## Statistical analyses

I used two approaches to study plant mobility. First, I calculated cumulative frequencies of individual species (percentage of subplots being occupied by a species until a given year) and cumulative species numbers (total number of species having been observed in the plot until a given year) at scales from 25 cm$^2$ to 2.25 m$^2$. These variables have also been used by other authors, and reflect plant mobility in a plot (Watt 1981; Sykes et al. 1994; van der Maarel & Sykes 1997). However, they do not take into consideration distances over which the plants move. Therefore, I introduced a new approach, calculating year-to-year distances between all pairs of subplots occupied by a species. A distance of 1 unit means the distance to one of the four neighbouring subplots, a distance of 2 units is the distance to a subplot at the other side of a neighbouring subplot, etc. The distances in units always refer to the smallest scale with subplots 5 cm × 5 cm. The observed values of cumulative species number (cumulative richness) and distances between sites of plant occurrence in particular years were compared with the expected ones based on a completely random model in which each species was distributed randomly over the subplots with

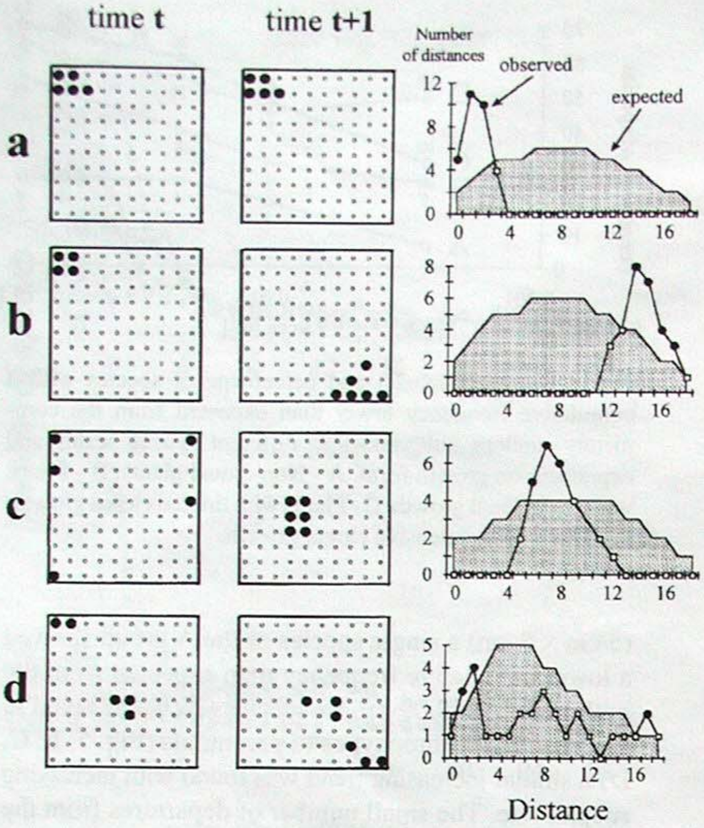

**Fig. 2.** Example of the analysis of year-to-year distances between subplots occupied by a single species: results for times $t$ and $t+1$ in a $10 \times 10$ lattice of subplots. The observed distribution of distances is compared with expected ones, indicated by an area delimited by the middle 95 % values calculated from randomized distribution at time $t+1$. ▫ = values not significantly different from expected ones; ● = values different from the expected ones at $\alpha = 0.05$.

**a.** Species (•) did not move between $t$ and $t+1$. Therefore, the number of distances of 0 to 2 units is higher than expected under the null model.

**b.** Plants moved to the distant corner of the lattice. Thus, an unexpectedly high number of long distances is found.

**c.** Plants spread closely along the margin of the square moved to its centre. Medium distances are over-represented.

**d.** Species occupied the centre and one corner of the square. At time $t+1$ it partly stayed in the centre and partly moved to the opposite corner. Thus, very short as well as long distances are more frequent than expected.

the frequency observed in the field. This model mimics the behaviour of a community consisting of annuals with random dispersal over the subplots (cf. van der Maarel & Sykes 1997). An example of the effect of year-to-year plant mobilities on the distribution of year-to-year distances is given in Fig. 2.

The completely random model is unrealistic for most perennial plants. Therefore, to predict cumulative species numbers, I developed a restricted random model. In this model the distribution of each species in the preceding years was taken into account in the following way: if the same frequency was observed in two successive years, the subplots occupied in the first year were also occupied in the second year. If the frequency in the second year was lower, then randomly generated subplots occupied in the first year were freed to obtain the number of occurrences observed in the second year. If the frequency in the second year was higher than in the first one, occurrences from the first year were used in the second year and the remaining occurrences were generated randomly. Frequency reduction results in a slight randomness whereas an increase in plant frequency generates a high randomness as newly occupied subplots are generated randomly. According to this model all species behave as non-clonal perennials: they persist at a spot in many cases; higher establishment or mortality rates are achieved only if large differences between year-to-year frequencies are observed. All simulations were carried out 2000 × to obtain probabilities for 2-tailed tests.

## Results

The mean number of vascular plant species recorded in the 1.5 m × 1.5 m plot between 1991 and 1997 was 65 and ranged from 58 (1991) to 72 (1995). The cumulative species number recorded until 1997 was 89. It increased linearly over the period of 7 yr (Fig. 3). The fit of the data by a logarithmic regression which should be high if a limited species-pool is available, did not increase the coefficient of determination. Linear trends of the cumulative species number were also found for subplots of

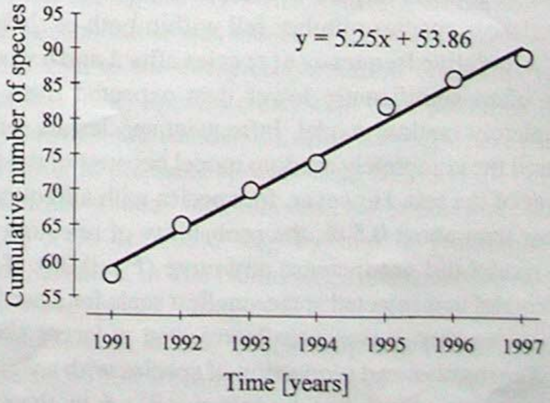

**Fig. 3.** Cumulative species richness recorded from 1991 to 1997 in the 1.5 m × 1.5 m plot. Linear regression provided a better fit than a logarithmic regression. The variable $x$ in the regression equation is the serial number of the year with $x = 1$ corresponding to 1991.

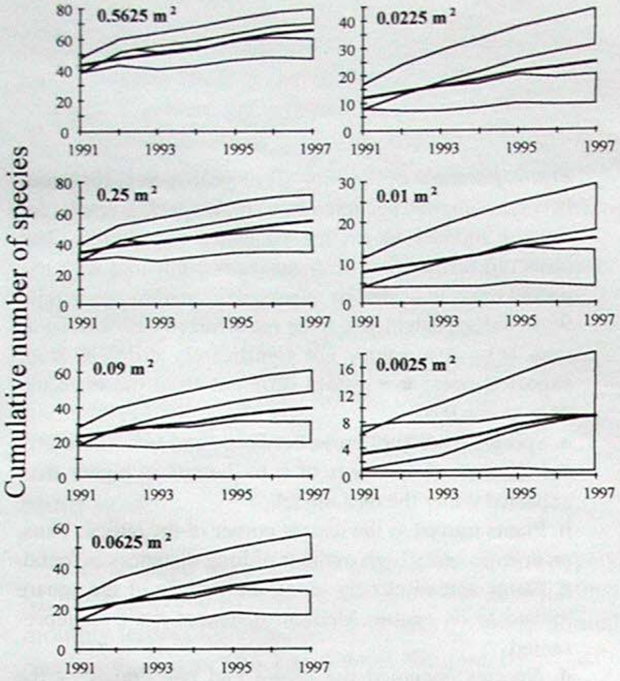

**Fig. 4.** Cumulative species richness recorded from 1991 to 1997 at scales 0.0025 m$^2$ to 0.5625 m$^2$. The envelopes are delimited by the middle 95 % of values of cumulative species number calculated from completely random (upper area) and restricted random (lower area) models. See text for details.

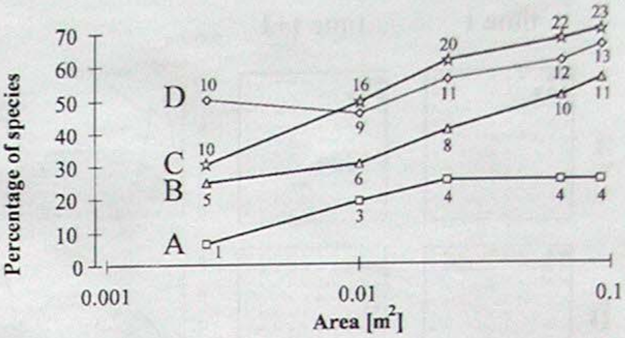

**Fig. 5.** Number (labels) and percentage of species with a cumulative frequency lower than expected from the completely random null model at different spatial scales and dependent on growth form. A - Non-clonal plants; B - Plants with poor clonal growth; C - Plants with limited clonal growth; D - Plants with extensive clonal growth.

various sizes (Fig. 4). At all scales, except the smallest one, there was a big difference in predicted cumulative numbers between the two models. The observed cumulative numbers were mostly between the ranges predicted by the two null models, but usually slightly closer to the null model with restricted randomness (Fig. 4). The width of the confidence envelopes increased for smaller subplots so that at the smallest scale (5 cm × 5 cm) the envelopes calculated from the two null models largely overlapped and the observed cumulative species number fell within both of them.

Cumulative frequency of species after 1 and 6 yr was very often significantly lower than expected from the completely random model. Infrequent species are rarely beyond the completely random model because of the low power of the test. However, for species with a frequency higher than about 0.5 %, the probability of rejecting the null model did not increase any more ($P > 0.05$). If the null model was rejected at the smallest scale for a particular species then it was usually rejected at larger scales too. The number and proportion of species with a significantly lower cumulative frequency after 6 yr than expected, strongly increased with subplot size and markedly differed according to growth form (Fig. 5). The lowest values were found in short-lived plants (A), independent of the spatial scale. At the smallest scale (5 cm × 5 cm) a single species of the A group showed a lower cumulative frequency than expected from the null model. At 0.09 m$^2$ six species (25 %) behaved in this way. In the three types of perennials (Fig. 5: B, C, D) a similar increasing trend was found with increasing subplot size. The small number of departures from the null model at smaller scales can partly be explained by the large number of plants with low frequencies. The behaviour of plants with poor clonal growth (B) was intermediate between the categories A and C+D. Surprisingly, there was little difference between plants with limited (C) and extensive (D) clonal growth, except for the smallest subplots where plants with extensive clonal growth differed from the null model more frequently than those with limited clonal spreading (Fig. 5).

The number of species with dynamics different from that predicted by the completely random null model was high (Table 1). Most plants persisted at a spot or spread to nearest distances more frequently than expected. Rarely, an unexpectedly low number of occurrences was found at medium distances, but this effect was a consequence of the fact that the plants spread over small distances only. The accumulation of plants at short distances inevitably resulted in their absence at medium distances. For the longest distances no departure from the null model was detected because the number of subsample pairs located at the opposite corners of the plot is small. The proportion of species deviating from the null model increased with decreasing scale (Table 1). The distribution of the year-to-year distances between sites of occurrence hardly differed between growth forms, whereas over longer time spans non-clonal plants were more mobile than clonal species (compare results for lags 1 and 6 in Table 1). The low number of departures from the null model in non-clonals was, however, partly caused by the low

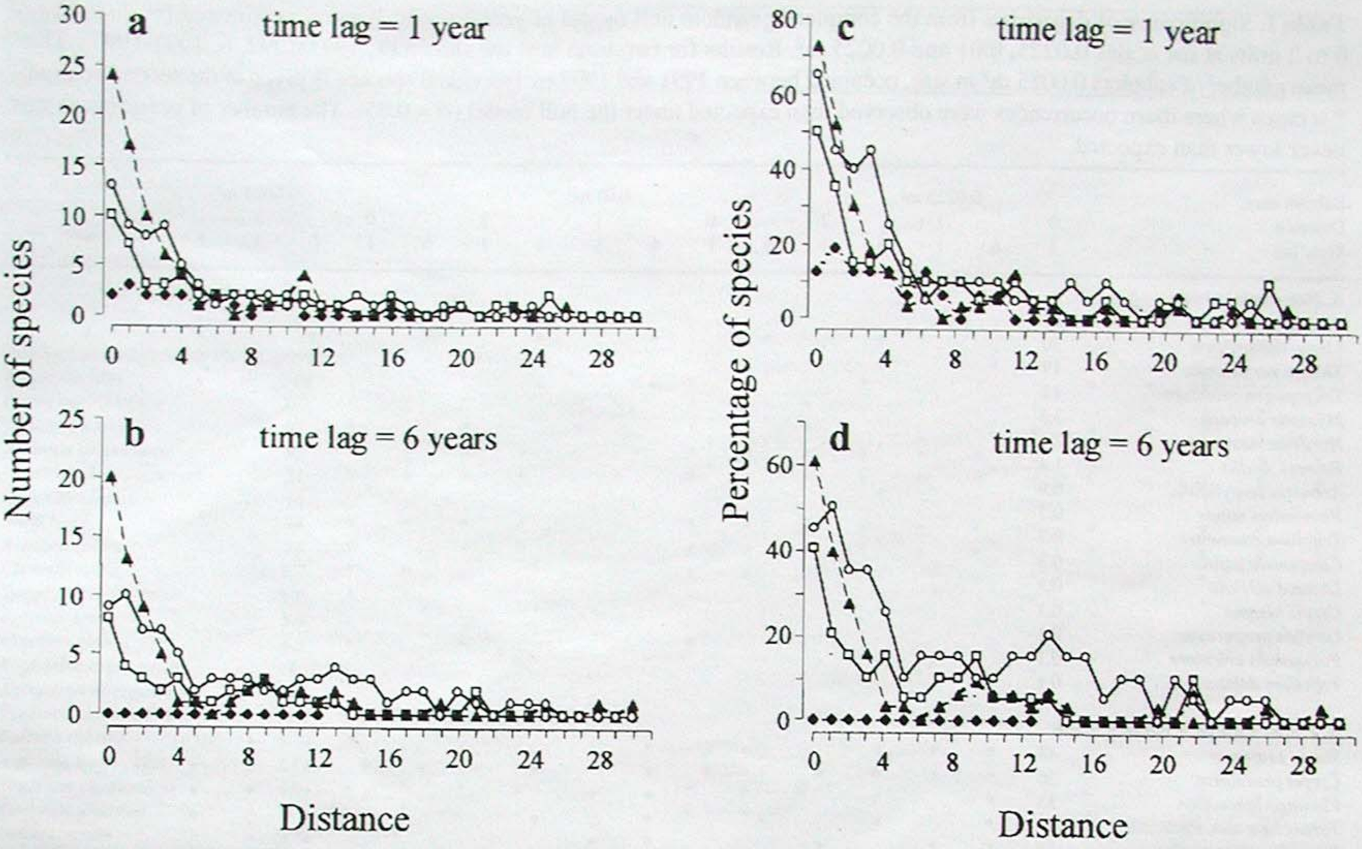

**Fig. 6.** Number (**a, c**) and percentage (**b, d**) of species found in 1992 (**a, b**) and in 1997 (**c, d**) at particular distances from the site of occurrence in 1991 more frequently than expected from the completely random null model; based on 0.0025 m$^2$ subplots. ···◆··· = Non-clonal plants; —□— = Plants with poor clonal growth; – –▲– – = Plants with limited clonal growth; —○— = Plants with extensive clonal growth.

frequency of most species belonging to this category and not by their high mobility.

The year-to-year persistence at a spot was higher than expected from the null model in 45 species (51 % of the total). The number and percentage of species differing from the null model decreased sharply with increasing distance. However, for distances of over six units the number and proportion of species for which the null model was rejected did not change any more (Fig. 6). There was hardly any difference between individual growth forms of clonal plants. At a time lag of 6 yr the percentage of species differing from the null model decreased in comparison with the 1991/2 results in all growth forms. Among annuals and biennials no species differed from the completely random null model at a time lag of 6 yr.

Curves for all clonal growth forms became less right-skewed with increasing time lags (Fig. 6). The relatively high values at longer distances indicate that after 6 yr spreading to a distance of up to 10 units can be expected in plants with poor and limited clonal growth and up to a distance of 16 units in plants with extensive clonal spreading.

## Discussion

The dynamics of the studied grassland differed from those predicted by the null models of completely random and restricted random models of year-to-year dynamics in several aspects. The cumulative species number recorded during the 7 yrs differed from both models at most scales, but it was closer to the restricted random model than to the completely random one. This indicates that many species either kept their positions over the years or established in the same subplot where plants belonging to the same species died. Sykes et al. (1994) found that annual accumulation of species recorded during 5 yrs decreased step by step in grasslands on Öland, Sweden, in The Netherlands and in the USA. The cumulative species number therefore followed a logarithmic function. A similar relationship was found for data from 1985-1995 from Öland (van der Maarel & Sykes 1997). In contrast, I found that the cumulative species number recorded during 7 yrs increased linearly at all studied spatial scales. The linear trend cannot persist for long periods because the number of established species is clearly limited by the size of the species pool

**Table 1.** Significance of departures from the completely random null model of year-to-year dynamics estimated for distances of 0 to 2 units at the scales 0.0225, 0.01 and 0.0025 m$^2$. Results for two time lags are shown (1: 1991-1992, 6: 1991-1997). The mean number of subplots 0.0025 m$^2$ in size, occupied between 1991 and 1997 by individual species, is given in the second column. * = cases where more occurrences were observed than expected under the null model ($\alpha = 0.05$). The number of occurrences was never lower than expected.

| Subplot area | | 0.0225 m$^2$ | | | | | | 0.01 m$^2$ | | | | | | 0.0025 m$^2$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Distance | | 0 | | 1 | | 2 | | 0 | | 1 | | 2 | | 0 | | 1 | | 2 | |
| Time lag | | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 |
| **A. Non-clonal plants** | | | | | | | | | | | | | | | | | | | |
| *Veronica arvensis* | 31 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Linum catharticum* | 20 | . | . | * | . | * | . | * | . | * | . | * | . | * | . | * | . | * | . |
| *Thlaspi perfoliatum* | 19 | * | . | * | . | . | . | . | . | * | . | * | . | * | . | * | . | * | . |
| *Tragopogon orientalis* | 12 | . | . | . | . | . | . | * | . | * | . | . | . | . | . | * | . | . | . |
| *Myosotis arvensis* | 3.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Hordeum murinum* | 2.6 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Bromus sterilis* | 1.4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Arenaria serpyllifolia* | 0.9 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Rhinanthus minor* | 0.7 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Trifolium campestre* | 0.7 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Campanula patula* | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Lactuca serriola* | 0.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Crepis biennis* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Lamium purpureum* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Polygonum aviculare* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Trifolium dubium* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| **B. Plants with poor clonal growth** | | | | | | | | | | | | | | | | | | | |
| *Salvia pratensis* | 43 | * | * | * | . | . | . | * | * | . | . | . | . | * | * | . | . | . | . |
| *Crepis praemorsa* | 36 | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * | * |
| *Plantago lanceolata* | 33 | * | . | * | . | . | . | * | * | . | . | . | . | * | * | * | . | . | . |
| *Taraxacum* sect. *Ruderalia* | 29 | * | . | * | . | * | . | * | . | * | . | . | . | * | . | * | . | . | . |
| *Peucedanum cervaria* | 14 | * | * | . | * | . | . | * | * | . | . | . | . | * | * | . | . | . | . |
| *Silene nutans* | 9.9 | * | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Trifolium montanum* | 7.7 | * | * | * | . | . | . | * | * | * | . | . | . | * | * | * | * | . | . |
| *Thesium linophyllon* | 6.6 | * | . | . | . | * | . | * | . | . | . | * | . | . | . | * | . | * | . |
| *Cerastium holosteoides* | 6 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Plantago media* | 6 | * | * | * | * | . | . | * | . | * | * | . | . | * | * | * | * | * | * |
| *Genista tinctoria* | 2.1 | . | . | . | . | . | . | . | * | * | . | . | . | * | * | * | * | . | * |
| *Scorzonera hispanica* | 1.9 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Crataegus monogyna* | 1 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | . | . | . | . |
| *Lotus corniculatus* | 0.6 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Trifolium pratense* | 0.4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Rosa gallica* | 0.4 | * | . | . | . | . | . | * | . | . | . | . | . | * | . | . | . | . | . |
| *Thymus pulegioides* | 0.4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Helianthemum ovatum* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Ononis spinosa* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Scorzonera purpurea* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| **C. Plants with limited clonal growth** | | | | | | | | | | | | | | | | | | | |
| *Bromus erectus* | 503 | * | . | . | . | . | . | * | . | . | . | . | . | * | * | * | * | * | . |
| *Carex montana* | 332 | * | * | . | . | . | . | * | * | * | . | . | . | * | * | * | * | * | * |
| *Molinia arundinacea* | 317 | * | . | * | * | . | . | * | * | * | * | * | . | * | * | * | * | * | * |
| *Festuca rupicola* | 124 | * | * | . | . | . | . | * | * | * | * | . | . | * | * | * | * | * | * |
| *Viola hirta* | 78 | * | . | . | . | . | . | * | . | . | . | . | . | * | * | * | * | . | . |
| *Filipendula vulgaris* | 68 | * | * | . | . | . | . | * | * | * | * | . | . | * | * | * | * | * | * |
| *Danthonia decumbens* | 67 | * | * | . | . | . | . | * | * | * | * | . | . | * | * | * | * | * | * |
| *Anthoxanthum odoratum* | 51 | * | . | . | . | . | * | * | . | . | . | . | * | * | . | * | . | . | . |
| *Dactylis glomerata* | 39 | * | . | . | . | . | . | * | * | . | . | . | . | * | * | * | * | * | * |
| *Cirsium pannonicum* | 37 | * | * | * | * | . | . | * | * | * | * | . | . | * | * | * | * | * | * |
| *Anthericum ramosum* | 24 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | * | * | * | * |
| *Primula veris* | 18 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | * | . | . | . |
| *Potentilla heptaphylla* | 15 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | . | . | . | . |
| *Campanula glomerata* | 12 | * | * | . | . | . | * | * | * | . | . | . | . | * | * | . | * | . | . |
| *Tanacetum corymbosum* | 9.9 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | * | * | . | . |
| *Arabis hirsuta* | 9.3 | * | . | * | . | . | . | * | . | * | . | . | . | * | . | . | . | . | . |
| *Pulmonaria angustifolia* | 7.4 | * | . | . | . | . | . | * | * | . | . | . | . | * | * | . | . | . | . |
| *Avenochloa pubescens* | 6.1 | * | . | . | . | . | . | * | * | * | * | . | . | * | * | * | . | * | * |
| *Lolium perenne* | 6 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Trisetum flavescens* | 4.7 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Rumex acetosa* | 4.6 | . | . | . | . | . | . | * | . | . | . | . | . | * | . | . | . | . | . |
| *Betonica officinalis* | 4 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | . | . | . | . |
| *Ranunculus polyanthemos* | 3.9 | . | . | . | . | . | . | * | . | . | . | . | . | * | . | . | . | . | . |
| *Centaurea jacea* | 2.4 | * | . | * | . | . | . | * | . | . | . | . | . | * | * | * | . | . | . |

| Subplot area | | 0.0225 m$^2$ | | | | | | 0.01 m$^2$ | | | | | | 0.0025 m$^2$ | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Distance | | 0 | | 1 | | 2 | | 0 | | 1 | | 2 | | 0 | | 1 | | 2 | |
| Time lag | | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 | 1 | 6 |
| *Knautia kitaibelii* | 1.7 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | * | * | . | . |
| *Arrhenatherum elatius* | 1.3 | . | . | . | . | . | . | * | . | . | . | . | . | . | . | * | . | . | . |
| *Pulmonaria mollis* | 1.3 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | . | . | . | . |
| *Vincetoxicum hirundinaria* | 0.7 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Hypochoeris maculata* | 0.4 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Briza media* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Gymnadenia conopsea* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Iris graminea* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Potentilla erecta* | 0.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| **D. Plants with extensive clonal growth** | | | | | | | | | | | | | | | | | | | |
| *Potentilla alba* | 319 | . | . | . | . | * | * | * | * | . | * | . | * | * | * | * | * | . | * |
| *Carex caryophyllea* | 257 | * | . | * | . | * | . | * | . | * | . | . | . | * | . | * | * | * | * |
| *Leontodon hispidus* | 97 | * | . | * | . | * | . | * | . | * | . | . | . | * | * | * | * | * | * |
| *Prunella grandiflora* | 43 | * | * | * | * | . | * | * | * | * | * | * | * | * | * | * | * | * | * |
| *Brachypodium pinnatum* | 31 | * | * | * | * | . | . | * | * | * | * | * | * | * | * | * | * | * | * |
| *Carex tomentosa* | 14 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Inula hirta* | 14 | * | * | * | * | . | . | * | * | * | * | * | * | * | * | * | * | * | * |
| *Achillea collina* | 13 | * | . | * | * | . | . | * | * | * | * | * | * | * | * | * | * | * | * |
| *Clematis recta* | 6.7 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | * | * | . | . |
| *Symphytum tuberosum* | 6.6 | * | * | . | . | . | . | * | . | . | . | . | . | * | . | . | * | . | . |
| *Agrostis tenuis* | 5.6 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Cruciata glabra* | 4.3 | * | . | * | . | . | . | * | . | * | . | * | . | * | . | * | . | * | . |
| *Euphorbia cyparissias* | 4 | . | . | . | . | . | . | . | . | . | . | * | . | * | . | . | . | . | . |
| *Agropyron intermedium* | 3.7 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Veronica chamaedrys* | 3.3 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Festuca rubra* | 3.1 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Asperula cynanchica* | 1.6 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |
| *Teucrium chamaedrys* | 1.6 | * | * | * | * | . | . | * | * | * | . | . | . | * | * | . | * | * | . |
| *Veronica teucrium* | 1 | * | * | . | . | . | . | * | * | . | . | . | . | * | * | . | . | . | . |
| *Galium verum* | 0.7 | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . | . |

(Pärtel et al. 1996; Zobel 1997; Zobel et al. 1998). However, the observed relationship may serve as evidence for a large species pool in the studied grassland. This corresponds well to the high species richness of vascular plants found in larger plots. For example, in a plot of 24 m$^2$, 103 species were recorded during a single visit close to the studied plot (Klimeš 1997). Moreover, the study plot is not as species-rich as some grasslands in the neighbourhood where up to 30 % more species have been recorded in 0.5 m$^2$ plots (Klimeš unpubl.). An alternative explanation of the linear increase of cumulative species number by directional changes of the grassland is not probable because the area is strongly protected, regular management has been used over decades there and no signs of successional changes have been recorded (Klimeš 1997).

Plant mobility is closely related to growth form (Herben et al. 1993, 1997). Species with long rhizomes or sprouting from roots are expected to be more mobile than plants with tap roots or short rhizomes (van der Maarel 1996; Herben et al. 1997). However, this holds for plants with an exclusively vegetative method of propagation. In reality there are great differences in the role of generative reproduction and in the success of plant establishment between clonal plants growing in grasslands (Ryser 1990, 1993; Rusch & van der Maarel 1992; Willems 1995). Therefore, the mechanisms behind the observed patterns in plant mobility may be more complicated.

Non-clonal plants, represented in the studied grassland mostly by annuals and biennials (category A), are certainly the most mobile members of the community. However, the only abundant species colonizing all subplots with the same probability as expected from the complete random null model was *Veronica arvensis* (Table 1). The behaviour of this species corresponded well to that of species of the assemblage of annuals studied by Geißelbrecht-Taferner et al. (1997). The habitat of the community studied by these authors was, however, much less covered by plants. Therefore, free movement of seeds was more likely there, resulting in all winter annuals behaving according to the null model.

Clonal plants with poor clonal growth (category B) persisted in individual subplots more often than was expected from the null model even after 6 yr. Some of the species never produced any seed (*Brachypodium pinnatum* and *Peucedanum cervaria*), because they started to flower just before they were cut. The life span of other plants, such as those belonging to *Taraxacum* sect. *Ruderalia*, is short (Vavrek et al. 1996, 1997), so that a fast turnover resulted in the rejection of the null model of plant mobility after one year, but not after 6 years (Table 1).

Nearly all abundant species with limited clonal growth (category C) persisted in their location more often than expected from the null model. Even after 6 yr they did not move often. This contrasts with the data from grasslands studied by Lieth & Ellenberg (1958) and van der Maarel & Sykes (1993) where most of the species are short-lived and more mobile. The effect of subplot size on the mobility in the studied plot was much higher in this group of species than in any other. The significant departures from the null model found at the smallest scale very often disappeared at larger scales (Table 1), especially for distances ≥ 1 unit at a time lag of 6 yrs). This indicates considerable plant mobility, however over small distances and longer time lags only. The probability of spreading to the nearest four or eight subplots 5 cm × 5 cm in size, was higher in this group of plants than in the previous group, corresponding to the expected behaviour of the two growth forms.

Plants with extensive clonal growth (category D) included numerous species spreading by means of long rhizomes and one species capable of producing buds and shoots on its horizontal roots (*Euphorbia cyparissias*; Rauh 1937). The mobility of these plants was not much higher than that of the previous group. The plants often persisted at a spot over the whole period of observation, but in some cases they produced descendants at distances up to 16 units (Fig. 6). The two abundant species not differing from the null model (*Carex tomentosa* and *Agrostis tenuis*, see Table 1) were not recorded in 1991. Their dynamics in the following years was similar to the other species. In *Prunella grandiflora*, *Brachypodium pinnatum*, *Inula hirta*, *Achillea collina* and *Clematis recta* the unexpectedly high number of short distances found in the analysis can be interpreted as the result of clonal spreading which seems to be quite effective. They never produced seeds because of the mowing regime. In other species (*Potentilla alba*, *Leontodon hispidus*, *Carex caryophyllea*) flowering and fruiting was frequent. Thus, the observed mobility may be partly caused by clonal growth and partly by generative reproduction.

Some species never flowered in the studied area. Among them *Asperula cynanchica*, *Euphorbia cyparissias*, *Teucrium chamaedrys* and *Veronica teucrium* should be mentioned. All of them belong to plants with potentially extensive clonal growth (category D; Kirchner et al. 1908-1936; Rauh 1937). Individuals of these species were rare in the whole plot and heavily suppressed during the whole period of observation. They were dwarfed and never reached the canopy of the stand. For example, all individuals of *Clematis recta*, a species with long rhizomes which grows up to 1.7 m in height in the area of Čertoryje and regularly bears hundreds of flowers per single plant (pers. observ.), were sterile in the studied plot, reached a height of 5 to 7 cm, and only produced 4 to 6 small leaves. The same holds for *Rumex acetosa* and *Vincetoxicum hirundinaria*, belonging to plants with limited clonal growth (category C; Rabotnov 1974). These species never flowered. *V. hirundinaria*, usually a robust plant up to 120 cm tall, was observed during 5 yrs as a single specimen at the same location, 3 to 4 cm high. These observations indicate that the role of asymmetric competition is low in the studied grassland. A similar conclusion was drawn for a calcareous grassland studied recently in the U.K. (Mahdi et al. 1989; Law et al. 1993; McLellan et al. 1997).

The overall number and proportion of clonal plants persisting at the same spot was high in the studied grassland. There was a trend of decreasing persistence with time lag. However, even after 6 yrs the persistence of all growth forms, except for annuals and biennials, was higher than expected under the completely random null model in more than 35 % of species. Moreover, the decrease of this proportion with time lag slowed down. Therefore, at least several decades will be needed for certain plants to reach any spot in the studied plot 1.5 m × 1.5 m in size. Many species spread to a distance of 1 or 2 units with a high probability, indicating that local spreading by clonal growth prevails in the studied community. The decrease of the importance of this local spreading with time was quite slow, if observable at all. Therefore, it will take a very long time before spreading to the nearest distances is as low as predicted by the completely random model. Similar population dynamics have been described from other plant communities, usually with sparse plant cover and with less above-ground biomass (Zoller & Stäger 1949; Zhang & Skarpe 1995, 1996; Winkler & Klotz 1997). Therefore, the results presented may serve as a first evidence that low plant mobility does not contradict high species richness even in plant communities with closed canopy and virtually no disturbance, other than mowing once a year.

Plant mobility is not directly linked with plant coexistence. However, a negative relationship between mean dry mass of ramets (above-ground biomass) and plant mobility (expressed as a 1-point correlation coefficient, see Herben et al. 1994) indicates that small plants which are usually inferior competitors are more mobile than larger plants which are competitively superior ($r = -0.354$, $p = 0.029$, $N = 37$; linear regression). Therefore, competitive exclusion of inferior plants may be postponed and plant coexistence promoted in this way.

In summary, the high mobility of species predicted for species-rich grasslands was not confirmed in the studied plot. In contrast, even those species which are equipped for fast and long-distance spreading by rhizomes, or which may produce shoots on roots, often do not utilise these possibilities. With the exception of annuals and a few species with frequent generative reproduction, the probability of occupying the same spot over several years was relatively high in the studied plant community. However, if the dynamics of individual species is summed up over decades, it could be possibly considered as high and nearly random.

## Conclusions

1. Nearly all species from the studied grassland are less mobile than expected from the completely random model.
2. In perennials there is a poor correlation between potential clonal growth and the observed species mobility.
3. Many species are apparently suppressed by the severe environment (temporal water and nutrient shortage combined with mowing) but this need not result in their elimination due to competitive exclusion for many years.
4. High plant mobility is probably not necessary for coexistence in species-rich grasslands, however it may promote coexistence.

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## References

Bell, A.D. 1984. Dynamic morphology: a contribution to plant population ecology. In: Dirzo, R. & Sarukhán, J. (eds.) *Perspectives on plant population biology*, pp. 48-65. Sinauer Assoc., Sunderland, MA.

Caswell, H. & Cohen, J.E. 1991. Communities in patchy environments: a model of disturbance, competition and heterogeneity. In: Kolasa, J. & Pickett, J.T.A. (eds.) *Ecological heterogeneity*, pp. 97-122. Springer, New York, NY.

Ehrendorfer, F. (ed.) 1973. *Liste der Gefäßpflanzen Mitteleuropas.* 2nd ed. Fischer, Stuttgart.

Geißelbrecht-Taferner, L., Geißelbrecht, J. & Mucina, L. 1997. Fine-scale spatial population patterns and mobility of winter-annual herbs in a dry grassland. *J. Veg. Sci.* 8: 209-216.

Glenn, S.M. & Collins, S.L. 1990. Patch structure in tallgrass prairies: dynamics of satellite species. *Oikos* 57: 229-236.

Glenn, S.M. & Collins, S.L. 1993. Experimental analysis of patch dynamics in tallgrass prairie plant communities. *J. Veg. Sci.* 4: 157-162.

Herben, T., Krahulec, F., Hadincová, V. & Kovářová, M. 1993. Small-scale spatial dynamics of plant species in a grassland community over six years. *J. Veg. Sci.* 4: 171-178.

Herben, T., Krahulec, F., Hadincová, V. & Pecháčková, S. 1997. Is a grassland communnity composed of coexisting species with low and high spatial mobility? *Folia Geobot. Phytotax.* 29: 459-468.

Hobbs, R.J. & Mooney, H.A. 1995. Spatial and temporal variability in California annual grassland: results from a long-term study. *J. Veg. Sci.* 6: 43-56.

Huston, M.A. 1994. *Biological diversity: the coexistence of species on changing landscapes.* Cambridge University Press, Cambridge.

Jongepierová, I., Jongepier, J.W. & Klimeš, L. 1994. Obnova druhově bohatých luk v Bílých Karpatech [Restoration of species-rich meadows in the Bílé Karpaty Mountains]. *Příroda* 1: 185-189. (In Czech.)

Kirchner, O., Löw, E. & Schröter, C. 1908-1936. *Lebensgeschichte der Blütenpflanzen Mitteleuropas.* Ulmer, Stuttgart.

Klimeš, L. 1995. Small-scale distribution of species richness in a grassland (Bílé Karpaty Mountains, Czech Republic). *Folia Geobot. Phytotax.* 30: 499-510.

Klimeš, L. 1997. Druhové bohatství luk v Bílých Karpatech [Species richness in grasslands in the Bílé Karpaty Mountains, Czech Republic]. *Sb. Prírodověd. Kl. Uherské Hradiště* 2: 31-42. (In Czech.)

Klimeš, L., Jongepier, J.W. & Jongepierová, I. 1995. Variability in species richness and guild structure in two species-rich grasslands. *Folia Geobot. Phytotax.* 30: 243-253.

Klimeš, L., Klimešová, J., Hendriks, R. & van Groenendael, J. 1997. Clonal plant architectures: a comparative analysis of form and function. In: de Kroon, H. & van Groenendael, J. (eds.) *The ecology and evolution of clonal plants*, pp. 1-29. Backhuys Publishers, Leiden.

Kull, K. & Zobel, M. 1991. High species richness in an Estonian wooded meadow. *J. Veg. Sci.* 2: 711-714.

Law, R., McLellan, A. & Mahdi, A.-K. S. 1993. Spatio-temporal processes in a calcareous grassland. *Plant Species Biol.* 8: 175-193.

Lieth, H. & Ellenberg, H. 1958. Konkurrenz und Zuwanderung von Wiesenpflanzen. *Z. Acker Pflanzenbau* 98: 205-223.

Mahdi, A., Law, R. & Willis, A. J. 1989. Large niche overlaps among coexisting plant species in a limestone grassland community. *J. Ecol.* 77: 386-400.

Maubon, M., Ponge, J.-F. & André, J. 1995. Dynamics of *Vaccinium myrtillus* patches in mountain spruce forest. *J. Veg. Sci.* 6: 343-348.

McLellan, A.J., Law, R. & Fitter, A.H. 1997. Response of calcareous grassland plant species to diffuse competition: results from a removal experiment. *J. Ecol.* 85: 479-490.

Økland, R.H. 1995. Persistence of vascular plants in a Norwegian boreal coniferous forest. *Ecography* 18: 3-14.

Palmer, M.W. 1994. Variation in species richness: towards a unification of hypotheses. *Folia Geobot. Phytotax.* 29: 511-530.

Pärtel, M. & Zobel, M. 1995. Small-scale dynamics and species richness in successional alvar plant communities. *Ecography* 18: 83-90.

Pärtel, M., Zobel, M., Zobel, K. & van der Maarel, E. 1996. The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos* 75: 111-117.

Rabotnov, T.A. 1974. *Biological flora of the Moscow Region.* Izdatelstvo Moskovskogo Universiteta, Moscow. 13 Vols.

Rauh, W. 1937. Die Bildung von Hypokotyl und Wurzelsprossen und ihre Bedeutung für die Wuchsformen der Pflanzen. *Nova Acta Leopoldina*, NF 4/24: 395-552.

Ricklefs, R.E. & Schluter, D. (eds.) 1993. *Species diversity in ecological communities.* The University of Chicago Press, Chicago, IL.

Rosenzweig, M.L. 1995. *Species diversity in space and time.* Cambridge University Press, New York, NY.

Rusch, G.M. & van der Maarel, E. 1992. Species turnover and seedling recruitment in limestone grassland. *Oikos* 63: 139-146.

Ryser, P. 1990. Influence of gaps and neighbouring plants on seedling establishment in limestone grasslands. *Veröff. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübel* 104: 1-71.

Ryser, P. 1993. Influences of neighbouring plants on seedling establishment in limestone grassland. *J. Veg. Sci.* 4: 195-202.

Stampfli, A. 1995. Species composition and standing crop variation in an unfertilized meadow and its relationship to climatic variability during six years. *Folia Geobot. Phytotax.* 30: 117-130.

Sykes, M.T., van der Maarel, E., Peet, R.K. & Willems, J.H. 1994. High species mobility in species-rich plant communities: an intercontinental comparison. *Folia Geobot. Phytotax.* 29: 439-448.

van der Maarel, E. 1996. Pattern and process in the plant community: fifty years after A. S. Watt. *J. Veg. Sci.* 7: 19-28.

van der Maarel, E. & Sykes, M.T. 1993: Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. *J. Veg. Sci.* 4: 179-188.

van der Maarel, E. & Sykes, M.T. 1997. Rates of small-scale species mobility in alvar limestone grassland. *J. Veg. Sci.* 8: 199-208.

van der Maarel, E., Noest, V. & Palmer, M.W. 1995. Variation in species richness on small grassland quadrats: Niche structure or small-scale plant mobility? *J. Veg. Sci.* 6: 741-752.

Vavrek, M.C., McGraw, J.B. & Yang, H.S. 1996. Within-population variation in demography of *Taraxacum officinale*: Maintenance of genetic diversity. *Ecology* 77: 2098-2107.

Vavrek, M.C., McGraw, J.B. & Yang, H.S. 1997. Within-population variation in demography of *Taraxacum officinale*: season- and size-dependent survival, growth and reproduction. *J. Ecol.* 85: 277-287.

Watt, A.S. 1981. Further observations on the effects of excluding rabbits from grassland A in East Anglian Breckland: the pattern of change and factors affecting it (1937-73). *J. Ecol.* 69: 509-536.

Willems, J.H. 1995. Soil seed bank, seedling recruitment and actual species composition in an old and isolated chalk grassland site. *Folia Geobot. Phytotax.* 30: 141-156.

Wilson, J.B. 1990. Mechanisms of species coexistence: twelve explanations for Hutchinson's 'paradox of the plankton': evidence from New Zealand plant communities. *N. Z. J. Ecol.* 13: 17-41.

Winkler, E. & Klotz, S. 1997. Long-term control of species abundances in a dry grassland: a spatially explicit model. *J. Veg. Sci.* 8: 189-198.

Zhang, W. & Skarpe, C. 1995. Small-scale species dynamics in semi-arid steppe vegetation in Inner Mongolia. *J. Veg. Sci.* 6: 583-592.

Zhang, W. & Skarpe, C. 1996. Small-scale vegetation dynamics in semi-arid steppe in Inner Mongolia. *J. Arid Environ.* 34: 421-439.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol. Evol.* 12: 266-269.

Zobel, M., van der Maarel, E. & Dupré, C. 1998. Species pool: the concept, its determination and significance for community restoration. *Appl. Veg. Sci.* 1: 55-66.

Zoller, H. & Stäger, R. 1949. Beitrag zur Altersbestimmung von Pflanzen aus der Walliser Felsensteppe. *Ber. Geobot. Forsch. Inst. Rübel Zür.* 1948: 61-68.

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