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A TRANSIENT EXPANSION OF SOWN PLANTS AND DIASPORE LIMITATION

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Abstract: Dispersal limitation was studied in a species-rich meadow (53–65 species of vascular plants per 1.1 m^2) to which a mixture of weeds was accidentally sown. Even if none of the sown species belonged to the local species pool, five species successfully established. Of them one persisted for 7 years, however declined from 41 individuals in 1995 to 1 individual recorded in 2001. These results can be interpreted as an evidence for short-term diaspore limitation. In contrast, long-term data indicate no diaspore limitation. Establishment of weeds in subplots with a lower number of species and individuals was higher than in other subplots, indicating that plant establishment in the studied open-canopy grassland is affected by the spatial pattern of present plants.

Keywords: Diaspore limitation, Expansion, Long-term study, Plant establishment, Short-term data, Species-rich meadow, Survival, Weeds

Nomenclature: KUBÁT et al. (2002)

INTRODUCTION

According to the current knowledge, many plant communities are dispersal-limited, as demonstrated by seed augmentation experiments showing that in about 50% of the cases addition of seeds to existing populations results in an increase of plant abundance (TURNBULL et al. 2000). However, as pointed out by ZOBEL & KALAMEES (2005; further cited as ZK) dispersal limitation given in literature is possibly over-estimated because most studies so far performed have been too short to account for a transitional presence of added plants. ZK suggested that long-term experimental studies would solve this problem. While it is evident that the prevailing duration of seed addition experiments, which is one to three years, is hardly sufficient for an unbiased estimation of dispersal limitation, it is less clear what the optimal duration would be.

The concept of dispersal limitation apparently suffers from other methodological drawbacks as well (ZK) and experimental designs to test it have been diverse and intervening factors numerous so that generalizations seem to be premature. For example, it is becoming evident that species of different origin behave in different ways so that it is worth treating them separately, e.g. using the hierarchical species pool concept (ZOBEL 1997), and gradients of productivity and disturbance should also be considered because limitation by diaspores markedly changes along them (TURNBULL et al. 2000, SEABLOOM et al. 2003, FOSTER et al.

2004). Successional status is another characteristic that may contribute to the diversification of plant communities according to dispersal limitation. To shed more light on dispersal limitation in plant communities, ZK proposed that long-term replicated diaspore addition experiments should be conducted in different environmental conditions with carefully selected sown species where the effects of various intervening factors are considered. A careful selection of target vegetation could also be added because many experiments, especially those designed to study various aspects of the functional role of biodiversity, are being performed using mixtures of forage and ruderal plants that represent artificial assemblages ("Euromixture") with a limited persistence and little resemblance to the natural vegetation. However, as pointed out by ZK, the demands for such experiments are rather high so that hardly any of the studies performed to date has accomplished all of them. Therefore, aside from the extensive experiments that will possibly be naturally restricted to highly artificial conditions, less complex studies are still valuable, as they may fill the gaps and extend our knowledge to marginal habitats and situations in which large experiments are not applicable due to logistic constraints.

The experimentally added seeds are usually selected according to the species pool of the target community. Therefore, it is expected that they accommodate within the target community easier than seeds of other plants, if competition, herbivory or diseases do not prevent plant establishment (ZOBEL 1997). However, those few studies in which added seeds belonged to different species pools gave inconsistent results. For example, PETRYNA et al. (2002) found that alien species cannot establish in undisturbed sites of mountain grasslands whereas disturbance of the ground and removal of native plants promotes their establishment. In contrast, LEVINE (2001) found that both exotic and native species established in intact and disturbed tussocks along a stream. Similarly, FOSTER & TILMAN (2003) reported that several sown species belonging to the "landscape species pool" persisted in an oak savanna grassland for 7 years. Due to a limited number of available studies it is impossible to evaluate the role of disturbance frequency and severity, and species pool delimitation based on results of these experiments. Moreover, it is not clear to which extent our knowledge is biased by results from short-term experiments that may exaggerate diaspore limitation.

In this note I report on a long-term observation of an unplanned sowing of weedy plants into a natural species-rich grassland where the number of vascular plants species per 1.1 m^2 ranged between 59 and 65 from 1994 to 2001. None of the sown species had ever been observed in the studied grassland from 1989 to 2004, however, they occur along roads, paths several hundred meters off the studied site, and abundantly also on arable land and in villages in the same landscape. Therefore, they clearly belong to a different species pool. Three questions are addressed:

(1) Can weedy plants establish in a well-managed species-rich meadow?

(2) Is there any difference in establishment of weeds when short- and long-term data are compared?

(3) Does establishment of weeds depend on the kind of vegetation present at a spot? Due to the special circumstances, the set-up of the experiment could not be precisely controlled so that it superficially resembled natural experiments, as defined by DIAMOND (1986), with all benefits and drawbacks.

STUDY AREA AND METHODS

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 during the last 10 years (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°. The grassland has not been fertilized in the past decades. It is dominated by *Bromus erectus*. In 2001 eleven species attained a frequency higher than 5%: *Bromus erectus* 74.0, *Carex caryophyllea* 50.4, *Plantago lanceolata* 33.3, *Carex montana* 31.8, *Potentilla alba* 25.3, *Festuca rupicola* 19.3, *Molinia arundinacea* 18.4, *Danthonia decumbens* 11.1, *Crepis praemorsa* 9.6, *Viola hirta* 7.3, *Filipendula vulgaris* 6.7; based on 450 subplots, 5 × 5 cm in size. Above-ground biomass ranged from 221 g/m^2 to 412 g/m^2 from 1994 to 2001 – mean value 333 g/m^2. A more detailed description of the species composition of the plot and the environment is given in KLIMEŠ (1999).

The permanent plot, 0.75 m × 1.5 m in size, was divided by a cord into 450 subplots of 5 cm × 5 cm. In these subplots, numbers of rooted vascular plant ramets were recorded during the second week of June, from 1994 to 2001, usually 1 to 3 weeks before the meadow was cut. For details on species richness and the number of individuals see KLIMEŠ (1999). In late summer 1994, after the census was finished, a cartload of grass with abundant weeds was dried in the area that included the permanent plot. The hay was afterwards carefully removed from the area, however in the course of drying and manipulation with the grass and hay, seeds of numerous plants were released in the area. Some of them germinated already in autumn 1994, other ones in the following spring, partly colonizing the permanent plot. Their fate in the permanent plot was followed until 2001, when the last individual of the introduced species was recorded.

The numbers of species were compared between subplots colonized by weeds in 1995 and other subplots using repeated measures of ANOVA, followed by LSD tests for multiple comparisons.

RESULTS

In 1995 about 20 weedy species established in an area of about 100 m^2, surrounding the permanent plot. Out of them 5 species represented by 21 individuals reached the permanent plot (*Bromus sterilis*, *Lactuca serriola*, *Lamium purpureum*, *Lolium perenne* and *Polygonum aviculare*). Examples of species established in the surroundings are *Chenopodium album*, *Conyza canadensis*, *Echium vulgare*, *Plantago major*, *Poa annua*, *Rumex crispus*, *Sisymbrium officinale*, *Stellaria media*, *Tripleurospermum inodorum* and *Veronica chamaedrys* s.str. *Lolium* included 62% of individuals of the weeds recorded in the permanent plot. It was also the only species that survived until the next year. It further expanded, being represented by 41 individuals in 1996, of which 16 individuals flowered and set fruit. In the course of the next 6 years the abundance of *Lolium* decreased linearly, to the last individual observed in 2001. In the course of the last three years no *Lolium* plant flowered in the study plot.

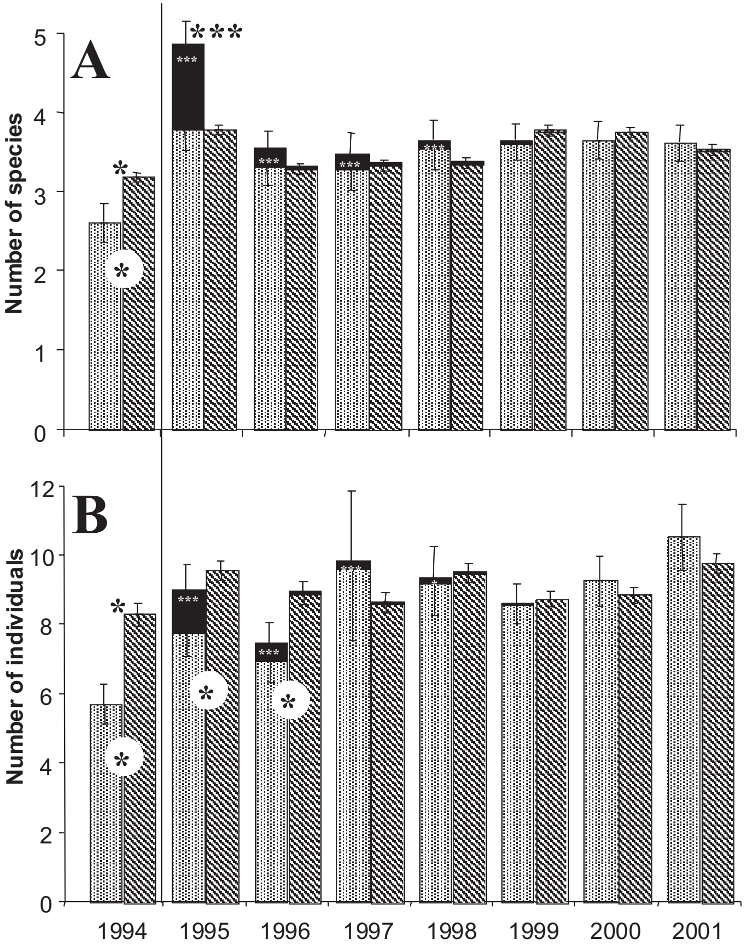

Fig. 1. Mean numbers (and s.e.) of local species (A) and individuals (B) recorded in subplots colonized (light) and not colonized by weeds in 1994 (grey). Mean numbers of weeds are in black. The vertical line separates the data obtained before and after sowing. Results of multiple comparisons are given for total number of species (above columns), weeds (within black columns) and local species (in white circles). * – $P < 0.05$, *** – $P < 0.001$.

The mean number of species and individuals in the subplots in which *Lolium* and other weeds were observed in 1995, was in 1994 lower than in subplots colonized by the weeds (Fig. 1). In 1995, the number of species in subplots that included the weeds was markedly higher than in other subplots, as a result of weed establishment. This difference diminished in 1996. When considering only local species, the number of species was the same in subplots colonized by weeds and other plots, however, the difference between the number of individuals of these two groups of plots persisted until 1996. Even if the number of subplots in which *Lolium* was observed gradually declined from 1996, this grass colonized new subplots until 2000. However, the mean number of species and individuals of weedy plants did not differ between plots initially colonized by weeds and those not colonized from 1999 to 2001. Thus, in the course of the last three years of observation, no difference in the mean number of species and individuals of sown plants between subplots initially colonized and not colonized by the weeds was found (Fig. 1).

DISCUSSION

Mechanisms regulating the dynamics of species-rich meadows are still poorly known. The role of above- and below-ground competition, resource partitioning, dispersal limitation, random processes, management practices and history has been appreciated, however, their relative contribution to the maintenance and persistence of high species richness is unknown. This study shows that establishment of species not belonging to the local species pool is possible even in extremely species-rich meadows, but their persistence is rather limited. With an exception of *Lolium perenne*, which was the only perennial plant among the sown weeds, all other species disappeared from the second to the third year after sowing. This could be interpreted as evidence for diaspore limitation (according to the definition by ZB). But because a strong environmental sieve (ZOBEL 1997) limited repeated recruitment, the diaspore limitation is doubtful from from a longer term perspective. Even if most weedy plants, not only those established in the study plot, flowered and set fruits (pers. observ.), their individuals were dwarfed and the number of released diaspores was apparently not sufficient to account for the losses due to the environmental limitations responsible for low germination and/or high seedling mortality. Numerous other plants naturally occurring in the studied meadows are often also suppressed and dwarfed (KLIMEŠ & KLIMEŠOVÁ 2002), but they adopt various mechanisms to prevent their extinction. These may include a long life-span, the ability to withstand stressful conditions in dry summers after mowing, which removes a large part of above-ground plant biomass, large carbohydrate reserves situated below ground, and a high mobility due to clonal growth and/or efficient dispersal of propagules, reducing the effect of diaspore limitation at a spot (KLIMEŠ 1999). None of the introduced weeds possessed any of these traits. Otherwise their expansion could have been successful, as documented by studies showing that increased and continuous input of seeds of weedy plants in small or fragmented natural habitats may break the function of the environmental sieve that prevents their persistence if seed input of weeds is occasional and small (REJMÁNEK 1996).

The successful establishment of *Lolium* was unexpected. This turf short-lived grass with a relatively large seed mass (1.79 mg; BURKE & GRIME 1996), readily germinating in standard conditions or after cold stratification (NIKOLAEVA et al. 1985), belongs to the less successful plants if sown into pastures (BURKE & GRIME 1996, BUCKLAND et al. 2001). Its demands for basic nutrients is relatively high (BEDDOWS 1967, ELLENBERG 1979) in comparison with all other plants recorded in the plot. Its ability to spread and colonize new subplots after its establishment in 1995 strongly supports the view that the studied community could relatively easily be invaded by numerous species, if their diaspores reach it, in accordance with the prediction by FOSTER et al. (2004) made for low productivity plant communities.

Interestingly, weed establishment was higher in subplots with a lower number of species and individuals. As these two variables are not independent of each other, they cannot be interpreted separately. They rather function as surrogates of plant biomass or an inverse of the proportion of open sites (gaps) (cf. PÄRTEL & ZOBEL 1995, HERBEN et al. 1997). Even if competition is probably not a crucial factor in unproductive grasslands (STAMPFLI 1995, ZOBEL 1997), shading and other effects caused by established plants may locally reduce the germination rate and establishment of seedlings because they are more sensitive to these factors than adult plants (KUPFERSCHMID et al. 2000).

Concluding, most species-rich plant communities, such as the studied meadow, may appear diaspore-limited when short-term data are used for the evaluation (cf. ZK), even if tested by adding seeds of plants not belonging to the local species pool. However, long-term data may provide a different picture. In spite of abundant flowering and fruiting virtually all sown plants diminished within seven years, including the perennial, but short-lived, *Lolium*. This implies that a transient presence of long-lived plants may extend in the same community for decades, before these populations decline. It is questionable whether diaspore limitation is still an appropriate term for such a situation. I suggest that besides considering separately the assignment of sown plants to the community, local, and regional species pools, as recommended by ZK, we should also carefully distinguish the ability of added species to germinate, establish individual plants and establish persisting populations. I believe that only the last case, which has been so far rarely demonstrated experimentally, indicates a real diaspore limitation relevant in the community.

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