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Seed availability in hay meadows: Land-use intensification promotes seed rain but not the persistent seed bank

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ABSTRACT

Intensification of land use in semi-natural hay meadows has resulted in a decrease in species diversity. This is often thought to be caused by the reduced establishment of plant species due to high competition for light under conditions of increased productivity. Sowing experiments in grasslands have found reliable evidence that diversity can also be constrained by seed availability, implying that processes influencing the production and persistence of seeds may be important for the functioning of ecosystems. So far, the effects of land-use intensification on the seed rain and the persistence of seeds in the soil have been unclear.

We selected six pairs of extensively managed (*Festuco-Brometea*) and intensively managed (*Arrhenatheretalia*) grassland with traditional late cutting regimes across Switzerland and covering an annual productivity gradient in the range 176–1211 $g m^{-2}$. In each grassland community, we estimated seed rain and seed bank using eight pooled seed-trap or topsoil samples of 89 cm^2 in each of six plots representing an area of c. 150 m^2. The seed traps were established in spring 2010 and collected simultaneously with soil cores after an exposure of c. three months. We applied the emergence method in a cold frame over eight months to estimate density of viable seeds.

With community productivity reflecting land-use intensification, the density and species richness in the seed rain increased, while mean seed size diminished and the proportions of persistent seeds and of species with persistent seeds in the topsoil declined. Stronger limitation of seeds in extensively managed semi-natural grasslands can explain the fact that such grasslands are not always richer in species than more intensively managed ones.

1. Introduction

Global maxima of plant-species richness at small spatial scales have been recorded in nutrient-poor semi-natural grasslands (Wilson et al., 2012). Such grasslands, including dry hay meadows and pastures which persist under extensive or low-intensive management (Dietl and Lehmann, 2006), strongly declined over the second half of the 20th century in Europe and their multiple biodiversity-related services were degraded due to changes in land use, such as abandonment or intensification of management (EEA, 2010). This often involved activities such as ploughing, seeding, herbicide and fertilizer applications, and early and high-frequent cutting, resulting in radical replacement of the former plant communities. A more moderate form of land-use change aimed at increasing the quality and quantity of fodder harvested from hay meadows by fertilization in combination with increased cutting frequency and grazing (Dietl and Lehmann, 2006). A decrease in plant-species diversity related with such change is often thought to be caused by reduced establishment success of species due to high competition for light in sites of increased productivity (Hautier et al., 2009). Sowing experiments in grasslands have found reliable evidence that diversity can also be constrained by seed availability (Foster and Tilman, 2003; Turnbull et al., 2000; Zeiter et al., 2006; Zobel et al., 2000), implying that processes influencing the production and persistence of seeds may be important for the functioning of ecosystems. The variation among sites in the population and community response to increased seed availability is strikingly large (Stein et al., 2008; Zeiter et al., 2006) and poorly understood. Unexplained among-site variation might result from differences in the ambient seed rain and the size of the pre-existing seed bank (Clark et al., 2007). In the context of climate change, knowledge of seed rain and seed banks is also important for an understanding of grassland resilience to extreme weather events, as reproductive output and seed persistence can

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be expected to affect community composition (Stampfli and Zeiter, 2004, 2008).

While the effects of the cessation of management on seed availability and the seed banks have been studied in the context of restoration (Bakker et al., 1996; Bekker et al., 1997; Valkó et al., 2011), there is very little information on how land-use intensification affects seed abundance. The maturation of seeds of many species may directly be hampered as an earlier date of starting mowing is often necessary in the context of massive intensification. However, if land-use intensification allows for seed maturation, the seed rain should increase because water and nutrients are less limited. While fertilization of plants grown in greenhouse monocultures has indeed increased seed production (e.g. Manning et al., 2009), fertilization studies in natural communities have revealed mixed results (Burkle and Irwin, 2010; Dainese, 2011; Smith et al., 1996). Land-use intensification also changes the species composition of communities, but the consequences of such change for the seed rain are not known. Lower numbers of seeds may result from the fact that species with larger seeds are common among those European flora which prefer habitats of higher productivity (Pärtel and Zobel, 2007). Moreover, introduced species of grasses in intensively managed grasslands may produce fewer seeds because they have been selected for their clonal growth capacity or bred for forage production (Marshall and Hides, 2000).

In addition to influencing seed-rain density, land-use intensification may also affect the size of the seeds in the seed rain. Seed size may differ across environmental gradients because of a link between two trade-offs, the size-number (Harper et al., 1970; Smith and Fretwell, 1974) and colonization–competition (Armstrong, 1976; Hutchinson, 1951) trade-off. Ideally, larger seed size would be favoured in more fertile habitats in which competition for light is higher, while smaller seed size would be favoured in habitats in which open spaces are created by small-scale disturbances (Pakeman et al., 2008). However, in the face of environmental hazards, the effect of more nutrients stored in reserves may also result in better survival of individuals of species with larger seeds (Westoby et al., 1996). As different processes may select for larger seeds in more or less fertile grasslands, and as more frequent disturbance due to higher cutting frequency would select for smaller seeds in intensively managed grasslands, it remains unclear whether seeds size differs between differently managed grasslands.

A potential difference in the intensity or predictability of disturbance between extensively and intensively managed grasslands may also influence the persistence of seeds in the soil. According to Fenner and Thompson (2005), the seasonally predictable drought in Mediterranean grassland does not select for annual grasses with a persistent seed bank, while unpredictable disturbances created by grazing tend to favour dicotyledons with persistent seeds. Seed persistence or accumulation in the soil may differ between the two land-use types due to different abundances of seed predators, different seed longevity and dormancy, and different soil characteristics affecting the survival of seeds such as soil moisture (Pakeman et al., 2012) or the presence of fungi (Mordecai, 2012).

Persistence of species in the soil seed bank has been classified according to the vertical distributions of seeds in the soil (Thompson et al., 1997). This method assumes that the depth-distribution of the seeds in the soil reflects seed longevity, in that species with a higher proportion of seeds in lower soil layers have greater seed longevity (Bekker et al., 1998a; Grandin and Rydin, 1998). This assumption, however, does not take into consideration the fact that gain and loss of seeds in soil seed banks are independent processes. A recent seed burial experiment (Saatkamp et al., 2009) found different mortalities of seeds of different species in the soil and showed that estimates of species persistence in a seed bank based on seed densities of different soil layers were in fact correlated with seed production, but not with seed longevity. Therefore, reliable information on the longevity of seeds would need, for example, burial experiments or direct age determination by ^{14}C dating, methods which are lengthy or expensive. A relatively easy way to estimate the proportion of persistent seeds in the soil is to compare the seed densities of soil samples containing the seed rain of the current year and persistent seeds in the soil with the densities of simultaneously caught seeds in traps containing only seed rain of the current year. This approach quantifies the proportion of seeds in the soil which are transient but cannot distinguish between short- and long-term persistent seeds (sensu Thompson et al., 1997). It has rarely been used (but see Jakobsson et al., 2006).

In this study, we simultaneously measured the size and the composition of the seed rain and the topsoil seed bank in twelve permanent grasslands across Switzerland, covering an annual productivity gradient in the range 176–1211 $\mathrm{g\,m^{-2}}$. Within limits of land-use intensification which allow most species to set seed before the first cut, we answer the following questions: (1) Does community productivity influence the density and diversity of the seed rain? (2) Is the size of the seeds in the seed rain related to community productivity? (3) Does community productivity influence density and diversity of the seed bank, or in particular, the proportion of persistent seeds and the proportion of species with persistent seeds in the soil? We further investigated whether productivity effects on seed rain and seed bank are consistent across major plant functional groups.

2. Method

2.1. Study sites

This study was performed in twelve temperate semi-natural grasslands across Switzerland (Table 1, supplementary data, Fig. S1). We chose pairs of extensively managed *Festuco-Brometea* and intensively managed *Arrhenatheretalia*-type grasslands, representing space-for-time substitutes of plant communities transformed by past-to-present land-use intensification (Ellenberg, 1996), in six regions so that each pair had similar climatic conditions. We selected grasslands which have been constantly used for haymaking and not ploughed during the past decades. The extensively managed grasslands are normally not fertilized and are mown once or twice a year. The more intensively managed grasslands, including 'low intensive' and 'moderately intensive' grasslands sensu Dietl and Lehmann (2006), are regularly fertilized with manure or slurry and mown once to three times a year, often followed by autumn grazing (Table 1). Land use was slightly intensified at one *Festuco-Brometea* site (Pree, fertilization by manure) and slightly extensified at one *Arrhenatheretalia* site (Zollikofen, cessation of fertilization) during the past decade. Our selection of sites excluded 'highly intensive' grasslands in which seed set of most species is prevented by early and high-frequent cutting (Dietl and Lehmann, 2006). High species richness qualified several of the extensively managed meadows as sites of national importance (Anonymous, 2010). At the Negrentino site (Stampfli, 1992; Zeiter and Stampfli, 2012), species richness equals current world records at small spatial scales (Wilson et al., 2012).

At each site, a soil profile was sampled using an Edelmann auger (core length 10 cm, diameter 6 cm) to determine soil characteristics (Table 1) such as soil strata, water storage capacity and soil type (sensu FAL, 2002) in spring 2010 (S. Tschumi 2012, unpubl. BA thesis, Universität Freiburg). We also determined pH, measured in water, and C/N ratio, using a C–N analyzer (Vario Macro, Elementar GmbH, Hanau, Germany), of five pooled soil cores (length 6–13 cm, diameter 1.8 cm) sampled with a sharpened tube at each site except at Thun (ten pooled cores of 3 cm in length).