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Endozoochorous dispersal, seedling emergence and fruiting success in disturbed and undisturbed successional stages of sheep-grazed inland sand ecosystems

Carsten Eichberg, Christian Storm, Angelika Schwabe*

Department of Vegetation Ecology, Darmstadt University of Technology, Schnittspahnstr. 4, D-64287 Darmstadt, Germany

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Abstract

This study examines the seedling emergence and fruiting success of plant species endozoochorously dispersed by sheep in a field experiment in a Koelerion glaucae area. We designed a factorial experiment (faeces/soil disturbance/successional stage/year) that mimics sheep-mediated microsites and analysed all occurring vascular plant species from September 2002–December 2004. The faeces samples were collected in the same ecosystem and additionally analysed in a common-garden experiment (seedling emergence potential). According to the latter, 28 vascular plant taxa were identified (on average 124 seedlings per 100 g air-dry sheep faeces). In the field, 15 species emerged directly out of faeces, only five of which were able to set seeds (the threatened species *Medicago minima*, *Phleum arenarium*, *Silene conica*, *Vicia lathyroides* and the non-threatened *Vulpia myuros*). Graminoid competitors were not able to set seedlings in the field but did so in the common-garden experiment (mainly *Carex hirta*). The total numbers of seedlings emerging out of faeces (5% of the potential) and reaching fruit ripeness (0.4%) were very low.

In the stage of seedling emergence, ten of 42 species were significantly influenced by faeces, 11 species by disturbance and two species by an interaction of the two treatment factors (*Bromus tectorum*, *Saxifraga tridactylites*). In the fruiting stage, two species profited by faeces (*Bromus tectorum*, *Vulpia myuros*) and two species by disturbance (*Erophila verna*, *Corynephorus canescens*). Overall, the density and diversity of fruiting individuals were significantly influenced by both treatment factors. The faeces factor showed a strong dependence on year (increasing effect on both dependent variables in the first year, decreasing effect in the second year). The disturbance factor is dependent particularly on successional stage (increasing effect especially in the later successional stage).

Our study revealed the paradox that threatened species with low nutrient demands are the most successful direct colonisers of sheep-faeces deposits. For them to reach the fruiting stage is rare but is of importance if new habitats are to be made accessible.

Keywords: Common-garden experiment; Generative reproduction; Graminoid competitors; Seedling recruitment; Sheep-generated gaps; Stress-tolerant ruderals: S–R

*Corresponding author.
E-mail address: schwabe@bio.tu-darmstadt.de (A. Schwabe).

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Introduction

There are many results concerning the use of sheep (and other livestock) as endozoochorous diaspore vectors for the improvement of degraded cultural or semi-natural habitats (Auman et al., 1998; Ghassali et al., 1998; Lehrer and Tisdale, 1956; Poschlod et al., 1998; Razanamandranto et al., 2004; Russi et al., 1992; Simao Neto et al., 1987). On the other hand, sheep are potential vectors of undesirable (invasive or weedy) species via faeces deposition (Cook, 1998; Fredrickson et al., 1997; Heady, 1954; Olson et al., 1997; Piggin, 1978; Wallander et al., 1995). While historically mainly agricultural interests have been the background of these studies, today nature conservation aims have come more into focus (Mouissie, 2004; Poschlod et al., 1998). There is evidence that the currently observed decline in phytodiversity in fragments of endangered habitats is partly attributable to the historical loss of livestock-dispersal vectors functioning as plant population links (Bruun and Fritzbøger, 2002; Poschlod et al., 1998). Recently, some authors have stressed an ambiguity as to whether endozoochorous diaspore input constitutes a potential benefit or a danger to threatened plant communities, since a mixture of target and non-target species is dispersed (Eichberg, 2004; Mouissie, 2004; Zehm et al., 2004).

From the large amount of germinable diaspores and the wide amplitude of species (mainly herbs and grasses) found in ungulate faeces, some authors have inferred that endozoochory is important for the plant population dynamics of open grazed habitats (Cosyns and Hoffmann, 2005; Malo and Suárez, 1995a; Pakeman et al., 2002; Ridley, 1930). However, the significance of diaspore dispersal for plant population dynamics can be understood only if post-dispersal processes are considered (Garrido et al., 2005; Grubb, 1977; Jordano and Herrera, 1995; Kollmann and Schill, 1996; Nathan and Muller-Landau, 2000; Rodríguez-Pérez et al., 2005). Existing studies dealing with the colonisation of sheep faeces (Auman et al., 1998; Mouissie, 2004; Sánchez and Peco, 2002; Welch, 1985) revealed low seedling emergence and low establishment rates of endozoochorously dispersed diaspores. Rapid desiccation of faeces pellets and competition by the established vegetation were suggested as important reasons for this.

Besides the direct effects of faeces (diaspore content) on reproductive success, indirect effects (nutrient content, mechanical effects) play a role in the colonisation of sheep-faeces microsites. Sheep faeces can cause nutrient enrichment of the underlying soil and an enhanced phytomass production (Sakadevan et al., 1993). According to the data of Bergmann (2004), who investigated subsamples of the faeces which were used for our experiments, the deposition of nutrients by a single layer of faeces pellets amounts to 290–380 kg N ha^{-1} and 71–89 kg P ha^{-1}. However, these nutrients are mostly in organic form and require mineralisation before they become available for plants. This process is slow if the sheep faeces desiccate (Floate, 1970). N mineralisation was reported to peak within the first 3 weeks after faeces deposition and to decline afterwards due to microbial immobilisation (Floate, 1970). The release of P follows the physical breakdown of sheep faeces (Rowarth et al., 1985). As in our climate the faeces decomposition was rather slow (see Results Faeces-borne seedlings in the field experiment (question 2)), we expect an initial pulse of mineral nitrogen, but only minor N and P release in the following months.

Another important feature of sheep-faeces deposits is their multi-pellet form, which generates conditions for embedded diaspores that are decisively different from conditions on faeces heaps produced by, e.g., cattle. Faeces consisting of a large number of small-sized pellets are prone to desiccation and will be relative easily pushed away by soil-borne ramets of the grazed plant community.

Habitat modification by large herbivores is inseparably accompanied by disturbance and the creation of gaps (e.g., Bakker and Olff, 2003; Bullock et al., 1994); with respect to sheep these are caused by faeces deposits, resting places, livestock trails and hoofprints. Herbivore-generated microsites might provide favourable conditions for seedling recruitment (Bakker, 2003; Eichberg et al., 2005). In many grasslands, including sand grassland (Jentsch, 2004; Schwabe and Kratochwil, 2004), gaps are required for successful recruitment of plants. In some herbivore-generated microsites (e.g., livestock trails), there is a spatial correlation between soil disturbance and faeces deposition. This can lead to directed dispersal effects (Bullock, 2000; Howe and Smallwood, 1982) and probably to an increase in plant-species richness at a local scale. Some authors have suggested that directed dispersal processes are more common than previously thought (Nathan and Muller-Landau, 2000; Wenny, 2001).

There is a lack of studies investigating dispersal processes in threatened plant communities and considering the whole regeneration process of all occurring vascular plant species.

In this study, we wanted to elucidate (1) the endozoochorous pathway of those species that were dispersed by sheep in sand pioneer vegetation (Koelerion glaucae Volk 1931: included in the Flora-Fauna-Habitat directive), a threatened habitat type in Central Europe bearing a large share of rare and threatened plant species (Ssymank et al., 1998) and (2) the impact of sheep-mediated microsites on Koelerion glaucae stands, i.e. the impact of faeces deposits as a whole and the impact of soil disturbances. We investigated the