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Original article

Survival and germination of Mediterranean grassland species after simulated sheep ingestion: ecological correlates with seed traits

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ABSTRACT

Large amounts of viable seeds from Mediterranean grassland species have been found in herbivore dung; however which species produce seeds that can survive and germinate after ingestion by herbivores is still not well understood. This paper evaluates the importance of seed size, shape and coat impermeability in the endozoochorous dispersal process of 20 abundant species from central Iberian rangelands. Seed survival, germination percentages and germination speed were analysed in controlled experiments on the chewing and gut passage process by inserting seeds in the rumen of fistulated sheep, followed by simulated acid–pepsin digestion. Higher germination percentages in the control than the simulated sheep ingestion treatment were found in 75% of seeds. All species showed lower survival following the treatment, two species had a higher germination speed and five had a lower rate. Large-seeded species generally had higher survival percentages than small-seeded species. Species with impermeable seed coats had higher germination percentages following treatment although no significant differences were noted for either seed survival or germination speed.

1. Introduction

Long-distance plant dispersal via herbivore endozoochory and exozoochory has been the focus of much attention in recent times due to the discovery that plant establishment in many systems is restricted by seed availability (e.g. Zobel et al., 2000; Foster and Tilman, 2003), the need to predict invasions (e.g. Myers et al., 2004) and to know the migration potential of species in the context of climate change (e.g. Cain et al., 1998; Pakeman, 2001; Watkinson and Gill, 2002), the effects of habitat fragmentations (e.g. Poschlod and Bonn, 1998; Higgins et al., 2003), and the success of restoration projects (e.g. Donath et al., 2003). However, we still lack general predictors, preferably based on easy to measure seed traits, for the likelihood of a seed being effectively transported via endozoochory, although several models for exozoochorous dispersal are already available (e.g. Romermann et al., 2005).

In order to predict the efficiency of species dispersal by endozoochory, we need to know which factors are important in determining the probability of ingestion by herbivores, the probability of survival and germination after ingestion and

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the effect of faecal material surrounding the seed, which may influence germination and seedling establishment. The mechanisms that regulate all of these aspects in the fate of a seed are still poorly understood. In this paper we focus on the effects of passage through an herbivore gut on the survival and germination of ingested seeds.

Large numbers of viable seeds from grassland species have been found in herbivore dung (Janzen, 1984; Malo and Suárez, 1995; Pakeman et al., 1998). Species with a wide range of apparent adaptations to dispersal, including those classified as being capable of unassisted dispersal, are obviously capable of endozoochorous dispersal as well (Pakeman et al., 2002). Although small seeds are much more likely to be found in herbivore dung (Russi et al., 1992; Pakeman et al., 2002; Couvreur et al., 2004), surveys have only yielded correlations that can be mediated by other causal explanations.

Experiments are better tools for analysing the association of plant traits with the probability of survival and changes in germination behaviour after gut treatments (Russi et al., 1992; Gardener et al., 1993; Malo and Suárez, 1996; Traveset et al., 2001; Manzano et al., 2005; Mouissie et al., 2005; Cosyns et al., 2005), although these rarely cover more than a few species of plants and herbivores. Attempts to generalise the effect of gut treatment on endozoochorous dispersal processes have detected a lack of information for non-fleshy fruited species and non-bird vertebrates (Traveset and Verdú, 2002), and there is still ample scope for further studies to test the emerging patterns.

The seed traits that are usually tested in experiments on the effect of gut passage on germination and survival of plant species are seed hardness, mass and shape. Legume seed survival after bovine digestion has been reported to be closely related to hard seed content (Gardener et al., 1993). Many studies have also found that ingestion reduces hardseededness, with a greater proportion of seeds capable of germinating after ingestion (Russi et al., 1992; Malo and Suárez, 1996), while other authors have found that this response is not ubiquitous and depends on the dispersed species and the dispersal vector (Traveset et al., 2001; Manzano et al., 2005; Cosyns et al., 2005). Experiments on the effect of gut passage have found that seed size is positively related to germination success (Traveset and Verdú, 2002; Cosyns et al., 2005), although a negative relationship has also been found in relation to seed survival (Mouissie et al., 2005). Finally, seed shape also shows a positive relation to germination success (Cosyns et al., 2005) and a negative relationship with survival (Mouissie et al., 2005). Elongated seeds seem to germinate more but survive less than rounded seeds.

The majority of small seeds passing through the digestive track of sheep are retained for 24–40 h (Manzano et al., 2005). During this time, they undergo a series of digestive processes. Firstly, the micro-organisms in the rumen-reticulum chamber trigger intense microbial fermentation. The unconsumed food matter and microbial cells are then attacked by the digestive enzymes in the stomach and the small intestine. The food not digested or absorbed then undergoes a new fermentation process in the large intestine with relatively little activity, and is ejected with the dung.

In this study we evaluated the importance of seed size, shape and seed coat impermeability in the endozoochorous dispersal by sheep of 20 abundant species in central Iberian rangelands. We analysed seed survival, germinability (final germination percentages) and germination speed using controlled experiments that simulated chewing and gut passage by a ruminant. For this we simulated seed damage by chewing and inserted seeds into the rumen of fistulated sheep, followed by acid–pepsin digestion.

Our hypotheses are that i) gut passage reduces survival in comparison with control seeds, and ii) seed mass, shape and seed impermeability influence survival and germination success.

2. Methods

2.1. Seed collection and seed traits

Between June and July 2003 we manually collected fully mature seeds from at least 20 individuals of 20 common grassland species in Central Iberian dry grasslands and scrublands, representing a range of seed sizes and shapes (Appendix 1). Prior to the simulated ingestion experiment, seeds were keep dry and in darkness at room temperature. Data for seed mass and shape were taken from Azcárate et al. (2002), where fresh seeds were collected between 1996 and 1999 in the same study area or measured directly in at least 20 individuals using the same methods. Seeds without any appendages were weighed (accuracy ±0.1 mg) and the three main dimensions were measured using image analysis equipment (Leica Q500Iw). Seed shape was calculated according to Thompson et al. (1993), as the variance of the three main dimensions after dividing all values by length. Totally spherical seeds would have shape = 0, with this value increasing as they became flatter or elongated. Seed coat impermeability was measured in a sample of 20 seeds per species, as 100 minus the percentage of imbibed or germinated seeds, after 2 days in distilled water (Baskin and Baskin, 2001). The method proposed by these authors involves weighing each seed to check changes in weight to measure imbibition. Due to the extremely small seed size of some of our species (e.g. *Juncus bufonius*), imbibition was checked via changes in size, measuring the first and second dimension using image analysis equipment (Leica Q500Iw). Seed impermeability was recorded in three classes: low, medium and high (values < 25%, 25–75%, > 75%).

2.2. Simulated herbivore consumption experiment

The seeds of each species were subjected to a simulated herbivore consumption treatment, in which the seeds were set to germinate after undergoing mechanical (simulated chewing) and chemical (simulated digestion) attack. Seeds were given two dry blows in a ceramic mortar to simulated chew-