GfÖ
GfÖ Ecological Society of Germany, Austria and Switzerland
Basic and Applied Ecology 17 (2016) 165–176
Basic and Applied Ecology
www.elsevier.com/locate/baae

How does gut passage impact endozoochorous seed dispersal success? Evidence from a gut environment simulation experiment

Tanja Milotić[a,*], Maurice Hoffmann[a,b]

[a]Terrestrial Ecology Unit, Department of Biology, Ghent University, Ghent, Belgium
[b]Research Institute for Nature and Forest, Department of Biodiversity and Natural Environment, Brussels, Belgium

Received 7 May 2015; accepted 16 September 2015
Available online 28 September 2015

Abstract

Endozoochory of temperate grassland species is a widespread phenomenon and may accelerate and/or increase germination in some plant species. However, the mechanisms causing this altered germination success are only partly understood. In this study, germination of common grassland species was evaluated after simulated herbivore digestion in a standardized lab environment. Ruminants (cattle) and hindgut fermenters (horses) were used as model organisms in this simulation experiment. Three major digestive processes were studied through mechanical, thermal and chemical treatments of the seeds simulating mastication, body temperature and digestive fluids, respectively. Congeneric groups of annuals and perennials were tested with 15 species belonging to the plant families Cistaceae, Cyperaceae, Fabaceae, Poaceae and Urticaceae. No differences between the impact of the simulated herbivore gut environments of cattle and horses could be found, but major differences in germination behaviour were found among plant species. For most of the tested plant species, treatments had a decelerating and inhibiting effect on germination compared to the untreated seeds. However, species of the Cistaceae and Fabaceae benefitted from mechanical treatments. Species of the Cyperaceae and Poaceae were hardly impaired by any of the treatments and even germinated better after chemical treatments. Thermal treatments, simulating the body temperature, prohibited germination in most cases. The germination success of *Urtica urens* was significantly higher after all treatments, which suggests seeds are specifically well adapted to gut passage, and hence to endozoochorous dispersal.

Zusammenfassung

Endozoochorie bei Graslandarten der gemäßigten Breiten ist ein weit verbreitetes Phänomen. Bei manchen Pflanzenarten könnte sie die Keimung beschleunigen und/oder verstärken. Indessen sind die Mechanismen, die diesen veränderten Keimungserfolg bewirken, nur teilweise bekannt. Wir untersuchten die Keimung von häufigen Graslandarten nach simulierter Verdauung durch Herbivoren in einer standardisierten Laborumgebung. Wiederkäuer (Rinder) und Dickdarmfermentierer (Pferde) standen Modell für die Simulation. Mastikation, Körpertemperatur und Verdauungssäfte wurden durch mechanische, thermische bzw. chemische Behandlung der Samen simuliert. Kongenerische Gruppen von ein- und mehrjährigen Pflanzen wurden getestet, insgesamt 15 Arten aus den Familien Cistaceae, Cyperaceae, Fabaceae, Poaceae und Urticaceae. Es gab keine Unterschiede zwischen den simulierten Herbivorenarten, wir fanden aber deutliche Unterschiede im Keimungsverhalten der untersuchten Pflanzenarten. In den meisten Fällen hatten die Behandlungen einen verzögernden oder hemmenden Effekt. Die Cistaceen- und

*Corresponding author. Tel.: +32 9 264 50 84.
E-mail address: tanja.milotic@ugent.be (T. Milotić).

http://dx.doi.org/10.1016/j.baae.2015.09.007

Fabaceenarten profitierten aber von den mechanischen Behandlungen. Die Cyperaceen- und Poaceenarten wurden kaum von den Behandlungen beeinträchtigt, ihre Keimung war nach chemischer Behandlung sogar verbessert. Thermische Behandlung, die die Körpertemperatur simuliert, verhinderte die Keimung in den meisten Fällen. Der Keimungserfolg von *Urtica urens* war nach allen Behandlungen signifikant erhöht, was nahelegt, dass ihre Samen besonders gut an die Darmpassage und damit an die endozoochore Ausbreitung angepasst sind.

Keywords: Endozoochory; Germination; Seed dispersal

Introduction

Seed dispersal is the link between the end of the reproductive cycle of the adult plant and the start of a new one by the establishment of offspring. It is one of the major drivers of vegetation composition as the process enables the colonization of new areas, maintains genetic diversity and has indirect implications on succession, regeneration and conservation (Wang & Smith 2002). According to the Janzen–Connell hypothesis seed dispersal is indispensable to enable the escape of seeds and seedlings from high density-dependent mortality caused by pathogens, seed predators, and/or herbivores in the direct vicinity of the parent plant (Janzen 1970; Connell 1971). This implies that those seedlings that are growing farthest from conspecific adults have a survival advantage. Dispersal agents are either abiotic (wind and water) or biotic (animals and the plant itself) and are related to diaspore morphology (Levin, Muller-Landau, Nathan, & Chave 2003). Animal mediated dispersal implies that seeds are attached externally (epizoochory) or ingested and dispersed in excreted dung (endozoochory). Many taxonomic groups have been reported to act as endozoochorous dispersers, including frugivorous birds (e.g., Wenny 2000), ants (e.g., Clarke & Davison 2001), beetles (de Vega, Arista, Ortiz, Herrera, & Talavera 2011), rabbits (e.g., Malo & Suarez 1995), foxes (D'hondt, Vansteenbrugge, Van Den Berge, Bastiaens, & Hoffmann 2011) up to the largest terrestrial herbivores (Campos-Arceiz & Blake 2011). Endozoochory by large herbivores could be one of the main mechanisms of long distance dispersal as a vast number of germinable seeds of many grassland species can be found in dung (e.g., Malo, Jimenez, & Suarez 2000; Pakeman, Digneffe, & Small 2002; Cosyns, Claerbout, Lamoot, & Hoffmann 2005; Couvreur, Cosyns, Hermy, & Hoffmann 2005). Furthermore, the combination of large home ranges, high travel velocity, large gut capacity and long seed retention time enables seeds to travel several kilometres away from the parent plant (Pakeman 2001; Nathan et al. 2008; Cousens, Hill, French, & Bishop 2010).

The survival of seeds in the digestive system is one of the main determinants of successful endozoochorous dispersal. Seed feeding experiments have resulted in contrasting outcomes with an increased germination success in some cases (e.g., Manzano, Malo, & Peco 2005; Ramos, Robles, & Castro 2006; D'hondt & Hoffmann 2011; Mancilla-Leyton, Fernandez-Ales, & Vicente 2011; Grande, Mancilla-Leytón, Delgado-Pertiñez, & Martín-Vicente 2013) and reduced germination in others (e.g., Cosyns, Delporte, Lens, & Hoffmann 2005; Manzano et al. 2005; Mouissie, Van der Veen, Veen, & Van Diggelen 2005; D'hondt et al. 2011; Grande et al. 2013). Successful endozoochorous dispersal is known to be related to both plant and herbivore traits (Albert, Mårell, Picard, & Baltzinger 2015). Plant traits such as diaspore size and shape, permeability or thickness of the seed coat, seed longevity and seed production (Pakeman et al. 2002; Cosyns & Hoffmann 2005; Mouissie et al. 2005; Bruun & Poschlod 2006), and herbivore traits such as diet, digestive system, seed retention time and body mass (Clauss et al. 2003; Cosyns & Hoffmann 2005; Van Weyenberg, Sales, & Janssens 2006) are important in determining whether seeds can be dispersed effectively through herbivore guts.

Mean retention time of seeds in the digestive system differs between ruminants and hindgut fermenters with generally longer mean retention times for horses than cattle (Cosyns, Delporte, et al. 2005). During the endozoochorical process, seeds are subjected to a range of digestive actions. During ingestion and rumination, the seeds may be abraded or crushed by the grinding action of the teeth. Also, seeds are held inside a warm and wet environment equalling the body temperature of the herbivore. Additionally, seeds are subjected to a wide range of chemical processes. Proteolytic and cellulolytic enzyme secreting bacteria can become attached to the seed surface in the rumen and large intestine of cattle (Gardener, Mcivor, & Jansen 1993b) and in the cecum and colon of horses (Householder, Gibbs, Potter, & Davison 1993), while in the abomasum or stomach and first part of the small intestine (duodenum), seeds are soaked in acid (pH 2–4) and exposed to proteolytic, amylolytic and lipotic enzymes (Gardener, Mcivor, & Jansen 1993a; Gardener et al. 1993b; Dijkstra, Forbes & France 2005).

In many studies, the endozoochorous dispersal potential of many plant species has been assessed experimentally by feeding a known number of seeds to herbivores or by germination trials of collected dung samples. However, many processes are influencing the germination success (e.g., density dependent germination, alternating environmental