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

Tanja Milotic´[a*,*](#_bookmark0)∗[,](#_bookmark2) Maurice Hoffmann[a*,*](#_bookmark0)[b](#_bookmark1)

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*

# 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 Keimungser- folg 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](mailto:tanja.milotic@ugent.be) (T. Milotic´).

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.

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***Keywords:*** Endozoochory; Germination; Seed dispersal

# Introduction

Seed dispersal is the link between the end of the reproduc- tive 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 coloniza- tion of new areas, maintains genetic diversity and has indirect implications on succession, regeneration and conservation ([Wang](#_bookmark48) [&](#_bookmark48) [Smith](#_bookmark48) [2002).](#_bookmark48) 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 herbi- vores in the direct vicinity of the parent plant ([Janzen](#_bookmark37) [1970;](#_bookmark37) [Connell](#_bookmark37) [1971).](#_bookmark37) 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,](#_bookmark39) [Muller-Landau,](#_bookmark39) [Nathan,](#_bookmark39) [&](#_bookmark39) [Chave](#_bookmark39) [2003).](#_bookmark39) Animal mediated dispersal implies that seeds are attached externally (epizoochory) or ingested and dis- persed in excreted dung (endozoochory). Many taxonomic groups have been reported to act as endozoochorous dis- persers, including frugivorous birds (e.g., [Wenny](#_bookmark50) [2000),](#_bookmark50) ants (e.g., [Clarke](#_bookmark19) [&](#_bookmark19) [Davison](#_bookmark19) [2001),](#_bookmark19) beetles ([de](#_bookmark17) [Vega,](#_bookmark17) [Arista,](#_bookmark17) [Ortiz,](#_bookmark17) [Herrera,](#_bookmark17) [&](#_bookmark17) [Talavera](#_bookmark17) [2011),](#_bookmark17) rabbits (e.g., [Malo](#_bookmark42) [&](#_bookmark42) [Suarez](#_bookmark42) [1995),](#_bookmark42) foxes ([D’hondt,](#_bookmark12) [Vansteenbrugge,](#_bookmark12) [Van](#_bookmark12) [Den](#_bookmark12) [Berge,](#_bookmark12) [Bastiaens,](#_bookmark12) [&](#_bookmark12) [Hoffmann](#_bookmark12) [2011)](#_bookmark12) up to the largest terrestrial herbivores ([Campos-Arceiz](#_bookmark18) [&](#_bookmark18) [Blake](#_bookmark18) [2011).](#_bookmark18) 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,](#_bookmark40) [Jimenez,](#_bookmark40) [&](#_bookmark40) [Suarez](#_bookmark40) [2000;](#_bookmark40) [Pakeman,](#_bookmark40) [Digneffe,](#_bookmark40) [&](#_bookmark40) [Small](#_bookmark40) [2002;](#_bookmark40) [Cosyns,](#_bookmark40) [Claerbout,](#_bookmark40) [Lamoot,](#_bookmark40) [&](#_bookmark40) [Hoffmann](#_bookmark40) [2005;](#_bookmark40) [Couvreur,](#_bookmark40) [Cosyns,](#_bookmark40) [Hermy,](#_bookmark40) [&](#_bookmark40) [Hoffmann](#_bookmark40) [2005).](#_bookmark40) Furthermore, the com- bination 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](#_bookmark30) [2001;](#_bookmark30) [Nathan](#_bookmark30) [et al.](#_bookmark30) [2008;](#_bookmark30) [Cousens,](#_bookmark30) [Hill,](#_bookmark30) [French,](#_bookmark30) [&](#_bookmark30) [Bishop](#_bookmark30) [2010).](#_bookmark30)

The survival of seeds in the digestive system is one of the main determinants of successful endozoochorous dis- persal. Seed feeding experiments have resulted in contrasting outcomes with an increased germination success in some

cases (e.g., [Manzano,](#_bookmark46) [Malo,](#_bookmark46) [&](#_bookmark46) [Peco](#_bookmark46) [2005;](#_bookmark46) [Ramos,](#_bookmark46) [Robles,](#_bookmark46) [&](#_bookmark46) [Castro](#_bookmark46) [2006;](#_bookmark46) [D’hondt](#_bookmark46) [&](#_bookmark46) [Hoffmann](#_bookmark46) [2011;](#_bookmark46) [Mancilla-Leyton,](#_bookmark46) [Fernandez-Ales,](#_bookmark46) [&](#_bookmark46) [Vicente](#_bookmark46) [2011;](#_bookmark46) [Grande,](#_bookmark46) [Mancilla-Leytón,](#_bookmark46) [Delgado-Pertin˜ez,](#_bookmark46) [&](#_bookmark46) [Martín-Vicente](#_bookmark46) [2013)](#_bookmark46) and reduced ger- mination in others (e.g., [Cosyns,](#_bookmark8) [Delporte,](#_bookmark8) [Lens,](#_bookmark8) [&](#_bookmark8) [Hoffmann](#_bookmark8) [2005;](#_bookmark8) [Manzano](#_bookmark8) [et al.](#_bookmark8) [2005;](#_bookmark8) [Mouissie,](#_bookmark8) [Van](#_bookmark8) [der](#_bookmark8) [Veen,](#_bookmark8) [Veen,](#_bookmark8) [&](#_bookmark8) [Van](#_bookmark8) [Diggelen](#_bookmark8) [2005;](#_bookmark8) [D’hondt](#_bookmark8) [et al.](#_bookmark8) [2011;](#_bookmark8) [Grande](#_bookmark8) [et al.](#_bookmark8) [2013).](#_bookmark8) Successful endozoochorous dispersal is known to be related to both plant and herbivore traits ([Albert,](#_bookmark13) [Mårell,](#_bookmark13) [Picard,](#_bookmark13) [&](#_bookmark13) [Baltzinger](#_bookmark13) [2015).](#_bookmark13) Plant traits such as diaspore size and shape, permeability or thickness of the seed coat, seed longevity and seed production ([Pakeman](#_bookmark31) [et al.](#_bookmark31) [2002;](#_bookmark31) [Cosyns](#_bookmark31) [&](#_bookmark31) [Hoffmann](#_bookmark31) [2005;](#_bookmark31) [Mouissie](#_bookmark31) [et al.](#_bookmark31) [2005;](#_bookmark31) [Bruun](#_bookmark31) [&](#_bookmark31) [Poschlod](#_bookmark31) [2006),](#_bookmark31) and herbivore traits such as diet, digestive system, seed retention time and body mass ([Clauss](#_bookmark21) [et al.](#_bookmark21) [2003;](#_bookmark21) [Cosyns](#_bookmark21) [&](#_bookmark21) [Hoffmann](#_bookmark21) [2005;](#_bookmark21) [Van](#_bookmark49) [Weyenberg,](#_bookmark49) [Sales,](#_bookmark49) [&](#_bookmark49) [Janssens](#_bookmark49) [2006)](#_bookmark49) are impor- tant 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,](#_bookmark8) [Delporte,](#_bookmark8) [et al.](#_bookmark8) [2005).](#_bookmark8) During the endozoochorical process, seeds are subjected to a range of digestive actions. Dur- ing 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 sub- jected 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 cat- tle ([Gardener,](#_bookmark26) [Mcivor,](#_bookmark26) [&](#_bookmark26) [Jansen](#_bookmark26) [1993b)](#_bookmark26) and in the cecum and colon of horses ([Householder,](#_bookmark34) [Gibbs,](#_bookmark34) [Potter,](#_bookmark34) [&](#_bookmark34) [Davison](#_bookmark34) [1993),](#_bookmark34) 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,](#_bookmark25) [Mcivor,](#_bookmark25) [&](#_bookmark25) [Jansen](#_bookmark25) [1993a;](#_bookmark25) [Gardener](#_bookmark25) [et al.](#_bookmark25) [1993b;](#_bookmark25) [Dijkstra,](#_bookmark25) [Forbes](#_bookmark25) [&](#_bookmark25) [France](#_bookmark25) [2005).](#_bookmark25)

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 ger- mination trials of collected dung samples. However, many processes are influencing the germination success (e.g., density dependent germination, alternating environmental

conditions, etc.) and can hardly be controlled in field con- ditions. In this study, the germination capacity and rate of common grassland species was tested after simulated herbi- vore digestion in a standardized lab environment. Ruminants (cattle) and hindgut fermenters (horses) were used as model organisms in this simulation experiment and three major digestive actions were studied through mechanical, thermal and chemical treatments simulating mastication, body tem- perature and digestive fluids. Congeneric pairs of grassland species from the Cistaceae, Cyperaceae, Fabaceae, Poaceae and Urticaceae which are known to be dispersed endozoo- chorically were used in order to find family or genus-related responses to our treatments. We hypothesize that early ger- mination in a highly competitive environment such as dung is beneficial for the survival and reproductive probabilities of the individual. We expect to find interspecific differences in germination rates and germinability, with faster and more germination in species which are frequently found germi- nating in dung samples (such as *Trifolium* and *Poa* species). Also, the mechanical treatments are expected to enhance ger- mination in hard seeded species, such as the tested species in the Cistaceae and Fabaceae.

# Materials and methods

## Plant species

Seeds of 15 grassland species belonging to five different families were used in this germination experiment. In most congeneric couples within each family an annual and a peren- nial species were selected (see [Appendix](#_bookmark9) [A:](#_bookmark9) [Table](#_bookmark9) [1](#_bookmark9) regarding selected species and seed origin). Most of the species are com- mon in temperate European grasslands and were previously found germinating in herbivore dung ([Cosyns,](#_bookmark6) [Claerbout,](#_bookmark6) [et al.](#_bookmark6) [2005;](#_bookmark6) [Cosyns](#_bookmark6) [&](#_bookmark6) [Hoffmann](#_bookmark6) [2005;](#_bookmark6) [Couvreur](#_bookmark10) [et al.](#_bookmark10) [2005;](#_bookmark10) [Cosyns,](#_bookmark10) [Bossuyt,](#_bookmark10) [Hoffmann,](#_bookmark10) [Vervaet,](#_bookmark10) [&](#_bookmark10) [Lens](#_bookmark10) [2006).](#_bookmark10) The Cis- taceae species were included because we presumed that their seeds were adapted to endozoochory. The abundance of the normally rare species *Helianthemum nummularium* remark- ably increased after the introduction of large herbivores in calcareous dune grasslands in Belgium (personal observa- tion Sam Provoost) and the germination rate is known to increase after gut passage ([D’hondt](#_bookmark12) [et al.](#_bookmark12) [2011).](#_bookmark12) The other species of the Cistaceae, *Cistus albidus* and *Tuberaria gut- tata*, have a Mediterranean distribution ([Thanos,](#_bookmark47) [Georghiou,](#_bookmark47) [Kadis,](#_bookmark47) [&](#_bookmark47) [Pantazi](#_bookmark47) [1992;](#_bookmark47) [Herrera](#_bookmark47) [2004)](#_bookmark47) and have been found to germinate from dung as well ([Malo](#_bookmark42) [&](#_bookmark42) [Suarez](#_bookmark42) [1995,](#_bookmark42) [1996).](#_bookmark42)

## Experimental treatments

The experiments were run during 2 periods of 100 days each. Five pre-germination treatment types were applied to the seeds, each representing steps in the digestive process in the gut system of horses or cattle (see [Appendix](#_bookmark9) [A:](#_bookmark9) [Table](#_bookmark9) [1).](#_bookmark9)

The first treatment group was the control group in which intact, untreated seeds were used as a reference to the other treatments (treatment “control”).

In the second set of treatments, seeds were treated mechan- ically in order to simulate the mastication process. Three different methods were used. A first set of seeds was scar- ified using fine grit sandpaper with average particle diameter of 125 µm. Seeds were put between two pieces of sandpaper which were moved twice (treatment “MS”). A second set of seeds was scarified using a cattle skull with the original teeth (treatment “MC”). On average the mastication intensity for cattle is 3.61 chews/g dry matter ([Janis,](#_bookmark35) [Constable,](#_bookmark35) [Houpt,](#_bookmark35) [Streich,](#_bookmark35) [&](#_bookmark35) [Clauss](#_bookmark35) [2010),](#_bookmark35) while [Erlinger,](#_bookmark22) [Tolleson](#_bookmark22) [and](#_bookmark22) [Brown](#_bookmark22) [(1990)](#_bookmark22) calculated that cattle consume on average 0.57 g of dry matter per bite. Combining both figures, seeds were chewed twice using a cattle skull. A third set of seeds was treated likewise using a horse skull (treatment “MH”). The average mastication intensity for horses is 4.61 chews/g dry matter ([Janis](#_bookmark35) [et al.](#_bookmark35) [2010)](#_bookmark35) and according to [Fleurance](#_bookmark23) [et al.](#_bookmark23) [(2009)](#_bookmark23) the intake rate (IR) can be defined by:

IR = −0*.*1972 + 0*.*0055 BM

where BM is the biomass of the grassland in g dry matter/m2. Using an average biomass of temperate dry and medium nutrient-rich grasslands of 206 g DM/m2 ([Tahmasebi](#_bookmark45) [Kohyani,](#_bookmark45) [Bossuyt,](#_bookmark45) [Bonte,](#_bookmark45) [&](#_bookmark45) [Hoffmann](#_bookmark45) [2008),](#_bookmark45) we concluded that chewing seeds four times with a horse skull would be a good simulation of mastication in this experiment. A third group of treatments dealt with the chemical scar- ification of seeds. It simulates the chemical abrasion of the seed coat in the stomach. The pH of the mixture of food and digestion fluids in the abomasum of cattle and the stomach of horses is highly dependent on the forage and physiological status of the animal and ranges between pH 2 and 4 for cattle ([Dijkstra](#_bookmark20) [et al.](#_bookmark20) [2005)](#_bookmark20) and between pH 1.5 and 4.6 for horses ([Murray](#_bookmark23) [&](#_bookmark23) [Schusser](#_bookmark23) [1993),](#_bookmark23) while the gastric retention time of ingesta ranges between 15 min and 2 h for cattle ([Dijkstra](#_bookmark20) [et al.](#_bookmark20) [2005)](#_bookmark20) and even up to 6 h for horses ([Van](#_bookmark49) [Weyenberg](#_bookmark49) [et al.](#_bookmark49) [2006).](#_bookmark49) During 15 min, a subset of seeds was put in a hydrochloric acid solution with pH 3.5 which falls within the range of previously reported concentrations of hydrochlo- ric acid in the abomasum and stomach of respectively cattle and horses (treatment “HCl”). In the abomasum and stomach both hydrochloric acid and pepsinogen are secreted. When the pH drops below 4, the pepsinogen gets activated into pepsin which breaks down proteins into peptides and amino acids ([Dijkstra](#_bookmark20) [et al.](#_bookmark20) [2005).](#_bookmark20) Therefore, a second and third set of seeds were put in a mixture of hydrochloric acid (pH 3.5) and 1% pepsin for 15 min (treatment “HCl-P15”) or 60 min (treatment “HCl-P60”), following the Tilley and Terry method ([Faithfull](#_bookmark24) [1984).](#_bookmark24) All chemically treated seeds were

rinsed with distilled water afterwards.

In the fourth group of treatments, the increased temperature during the passage through the intestinal system was simu- lated. Both cattle and horses have a constant body temperature of 38 ◦C ([Brown-Brandl,](#_bookmark15) [Eigenberg,](#_bookmark15) [Nienaber,](#_bookmark15) [&](#_bookmark15) [Hahn](#_bookmark15) [2005;](#_bookmark15)

[Green,](#_bookmark15) [Gates,](#_bookmark15) [&](#_bookmark15) [Lawrence](#_bookmark15) [2005),](#_bookmark15) while the retention time of seeds in the intestinal system differs among herbivore species. According to [Cosyns](#_bookmark7) [(2004)](#_bookmark7) germinating seeds were found after a mean retention time of 49 and 55 h for cattle and horses, respectively, with a minimal and maximal retention time of 24 and 72 h for cattle, and 24 and 96 h for horses. Therefore, four thermal treatments were tested putting intact seeds in Eppendorf tubes filled with distilled water in a warm water bath at a constant temperature of 38 ◦C for 24, 49, 55 and 72 h (treatments “T24”, “T49”, “T55” and “T72”, respectively).

In the fifth group of treatments, a combination was made of the mechanical, chemical and thermal treatments for cattle and horses separately. In the combination treatment for cat- tle (treatment “combiC”) treatments MC, HCl-P15 and T49 were executed consecutively, while in treatment “combiH”, the horse treatments MH, HCl-P15 and T55 were combined. For all species at least one of the treatments within each treatment group was applied. The same day the treatments were finished, 50 seeds per replicate were sown at equal dis- tance in Petri dishes filled with 1% water agar. In order to prevent evapotranspiration, the Petri dishes were closed with Parafilm tape. Per treatment and per species five replicates were used and all Petri dishes were arranged in a complete random design in a germination chamber with day: night fluctuating temperatures between 14 ◦C and 30 ◦C with a 12 h day:12 h night period. Light was provided by white fluorescent tubes (Sylvania, 36 W, Germany) with a light intensity (photosynthetic active radiation, PAR) between 10 and 45 µmol/m2 s depending on the location on the rack. Dur-

As the data for both MTG and germinability are nested structures with each species belonging to one family, a nested ANOVA was performed with MTG or germinability as mea- sured variable and treatment, life strategy and family as nominal variables with a nested family: species term. In order to meet the assumptions of parametric tests, MTG and germinability data were transformed using a log(*x* + 1) and asin(sqrt(*x*/100)) function, respectively.

One-way ANOVAs were performed per species in order to gain insight in the treatment effects per species and Tukey post hoc tests were applied in order to distinguish between significantly differing treatments.

Recently, time-to-event or survival analysis was proposed as a more solid statistical method coping with the timing of germination ([Onofri,](#_bookmark27) [Gresta,](#_bookmark27) [&](#_bookmark27) [Tei](#_bookmark27) [2010;](#_bookmark27) [McNair,](#_bookmark27) [Sunkara,](#_bookmark27)

[&](#_bookmark27) [Frobish](#_bookmark27) [2012).](#_bookmark27) The advantage of using these methods is that the timing of events (in this case germination) which occurs over time can be analysed including the effects of different factors (e.g., treatments). Our germination data are of the interval type with time intervals between two suc- cessive germination records varying between 1 and 14 days implying that the actual germination takes place between two successive germination observations. Seeds not germinated at the end of the experiment were considered as “right- censored” observations as they were expected to germinate at an unknown moment after the end of the experiment.

The germination probability was estimated non- parametrically by the Kaplan–Meier method:

ing the first 4 weeks of the experiments, newly germinated seeds were counted five times per week, while the counting effort was lowered to once in every 2 weeks once the majority

*s* (

*S*(*t*) = n 1 −

*j*=1

*dj* \

*nj*

of seeds had germinated. After each seed counting, the Petri dishes were put back in a new randomized sequence in order to avoid interference with possible unequal abiotic conditions in the germination chamber. Germination was considered to occur whenever a white radical emerged through the testa. Germinated seeds were discarded after counting in order to prevent interference with the remaining seeds.

## Data analysis

After finishing the experiments, the count data were con- verted to germinability and mean time per germination (MTG). Germinability can be defined as the cumulative per- centage of seeds that have germinated by the end of the experiment, while MTG was calculated as:

where *dj* is the number of seeds germinating in a given interval of time *j*, *nj* is the number of seeds “at risk” of germination in the same interval, which is the number of non-germinated seeds entering the interval minus one half of the number of seeds germinated during the same interval ([Venables](#_bookmark51) [&](#_bookmark51) [Ripley](#_bookmark51) [2002).](#_bookmark51) The germination probability was calculated for each treatment and species using the function *survﬁt* in the R environment.

Comparisons among germination curves were performed using AFT (accelerated failure time) regressions using the *survreg* function in R. Exponential, Weibull, Log-Normal and Log-Logistic distributions were tested per species. As suggested by [Onofri](#_bookmark27) [et al.](#_bookmark27) [(2010)](#_bookmark27) the problem of clustering of seeds within randomization units (Petri dishes) was over- come by adopting a frailty approach with Petri dishes as the clustering (gamma distributed) random effect. The second

MTG =

*k*

*i*=1

*di* ∗ *n*1

order Akaike’s information criterion (AICc) and a graphical

comparison of the model outcome with the Kaplan–Meier

*N*

where *di* is time from the start of the experiment to the *i*th observation, *ni* is the number of seeds germinated within the period *i*, *N* is the total number of germinated seeds during the experiment and *k* is the last time of germination ([Ranal](#_bookmark39)

[&](#_bookmark39) [Garcia](#_bookmark39) [De](#_bookmark39) [Santana](#_bookmark39) [2006).](#_bookmark39)

estimator were used to select the best fitting model for each species.

Using the method of [Onofri](#_bookmark27) [et al.](#_bookmark27) [(2010),](#_bookmark27) time ratios were derived from the AFT models. In this method, the germination time after each treatment is compared to the control treatment which has a time ratio of 1. Treatments with a time ratio

higher than 1 resulted in increased germination time, while treatments with a lower time ratio than the control treatment have lower germination times.

All analyses were performed with R version 3.1.2 ([R](#_bookmark41) [Core](#_bookmark41) [Team](#_bookmark41) [2014)](#_bookmark41) using the packages “survival” version 2.38-1 and “agricolae” version 1.2-1.

# Results

## Mean time to germination and germinability

Treatments had a significant effect on both the mean time to germination (MTG) and germinability ([Table 1).](#_bookmark3) Further- more, MTG and germinability differed significantly between plant families and between species within families, while different life strategies had only an effect on germinability ([Table 1).](#_bookmark3)

When comparing the MTG for the untreated (control) seed lot, the tested species in the Cistaceae, Cyperaceae and Urticaceae significantly needed more time to germinate than species of the Fabaceae and Poaceae (see [Appendix](#_bookmark9) [A:](#_bookmark9) [Table](#_bookmark9) [2).](#_bookmark9) Furthermore, germinability differed between plant fam- ilies with low germination percentages for species in the Cistaceae, while most seeds germinated in the Fabaceae and Poaceae ([Table 2](#_bookmark5)). However, within several plant families germinability differed significantly between tested species, while no clear correlation was found between life strategy and germinability. No significant differences were found between both simulated herbivores (cattle and horse) for the mechan- ical (MC and MH), thermal (T49 and T55) and combination treatments (combiC and combiH) ([Table 2).](#_bookmark5)

No significant differences were found between treatments in the Cistaceae for MTG, while the mechanical treatment using sandpaper resulted in higher germinability for both

*C. albidus* and *H. nummularium* ([Table 2](#_bookmark5)). Furthermore, significantly fewer seeds germinated following both heat treatments in *C. albidus*. None of the treatments had a signif- icant effect on the Cyperaceae species. Thermal treatments had an adverse effect on the germinability of the *Tri-* *folium* species and *Medicago lupulina* (T72). The chemical

**Table 1.** Results of nested ANOVAs with consecutively mean time to germination (MTG) and germinability as measured variable and treatment, life strategy and family as nominal variables with a nested family: species term.

Measured variable Factor df *F* value *p*

MTG Treatment 12 6.614 <0.001

Life strategy 1 0.039 0.843

Family 4 62.994 <0.001

Family: species 9 30.700 <0.001

Germinability Treatment 12 29.499 <0.001

Life strategy 1 43.343 <0.001

Family 4 257.607 <0.001

Family: species 9 45.830 <0.001

treatment HCl-P60 resulted in lower germinability for *Tri- folium repens* while both combination treatments resulted in lower germinability for all *Trifolium* species. All treatments except MH resulted in a higher germinability compared to the control treatment for *Urtica urens*, while no significant dif- ferences were found between the treatments for *Urtica dioica* ([Table 2).](#_bookmark5)

## Survival analysis

[Fig. 1](#_bookmark4) compares the germination probabilities of the treat- ments with the control treatment. These survival curves depict the germinability and time to germination which differed greatly between species. For most of the tested species the sur- vival curves of the treated seeds differ significantly from those of the untreated seed lots. Cistaceae species were mainly affected by mechanical and thermal treatments and to a lesser extent by chemical treatments, thermal treatments signifi- cantly altered the germination curves of all Fabaceae species except *Medicago arabica*. All applied treatments had a sig- nificant effect on the germination probability of *U. urens*, while the congeneric species *U. dioica* was only affected by the T55 treatment ([Fig. 1).](#_bookmark4)

The time ratio which compares the germination times of the treated seeds with those of the reference seed lot (control treatment) for each species indicates a decelerating germi- nation following the thermal and combination treatments for the tested Fabaceae species except *M. arabica* (see [Appendix](#_bookmark9) [A:](#_bookmark9) [Table](#_bookmark9) [3).](#_bookmark9) A clear difference was found for *U. urens* where any treatment accelerated germination. Chemical treatments had mainly an accelerating effect on *Carex ﬂacca* and both *Poa* species.

# Discussion

Most of the treatments had a decelerating and inhibiting effect on germination compared to the untreated seeds for most tested species. Species of the Cyperaceae and Poaceae were hardly impaired by any of the treatments and even germinated better after chemical treatments. Thermal treat- ments, simulating the body temperature, prohibited germina- tion in most cases. The germination success of *U. urens* was significantly higher under all treatments, while species of the Cistaceae and Fabaceae particularly benefitted from mechan- ical treatments. Nevertheless, accelerated germination might be beneficial, especially in competitive environments ([Orrock](#_bookmark28)

[&](#_bookmark28) [Christopher](#_bookmark28) [2010).](#_bookmark28) Dung pats can contain high numbers of endozoochorically dispersed seeds (e.g., [Cosyns,](#_bookmark6) [Claerbout,](#_bookmark6) [et al.](#_bookmark6) [2005),](#_bookmark6) and can therefore be regarded as highly compet- itive environments where early germinating individuals can benefit from the vegetation-free and nutrient-rich environ- ment of the dung pat ([Verdu](#_bookmark49) [&](#_bookmark49) [Traveset](#_bookmark49) [2005).](#_bookmark49)

The endozoochorous dispersal potential differs between species and depends on plant traits such as diaspore release height, and the morphology of the ingested diaspores.

1.00

***Carex acuta***

1.00

***Carex flacca***

1.00

***Cistus albidus***

**#**

**#**

1.00

***Helianthemum nummularium***

**# #**

**# #**

1.00

***Medicago arabica***

0.75

**Probability of not germinating**

0.75

**#**

0.75

0.75

**#**

**#**

0.75

**#**

**#**

**p<0.001**

*(MS, HCl−P60)*

0.50

0.50

0.50

0.50

0.50

0.25

**p=0.004**

0.25

**p<0.001**

0.25

**# #**

**# #**

**#**

**p<0.001**

0.25

**p<0.001**

0.25

0.00

*(HCl−P60)*

0 25 50 75 100

**Time (day)**

0.00

*(MS, MC, HCl, HCl−P60, T72)*

0 25 50 75 100

**Time (day)**

0.00

*(MS, T24, T72)*

0 25 50 75 100

**Time (day)**

0.00

*(MS, MC, HCl−P60, T24, T72)*

0 25 50 75 100

**Time (day)**

0.00

0 25 50 75 100

**Time (day)**

1.00

***Medicago lupulina***

**#**

1.00

***Poa annua***

1.00

***Poa pratensis***

1.00

***Trifolium arvense***

**# # #**

1.00

***Trifolium campestre***

**#**

**# #**

**#**

**#**

**#**

**p<0.001**

*(MH, T49, T55, combiC, combiH)*

0.75

**Probability of not germinating**

0.75

0.75

0.75

0.75

0.50

0.25

0.50

**#**

**#**

0.25

**#**

0.50

**#** 0.25

**#**

**# #**

**# # #**

0.50

0.25

**#**

0.50

0.25

0.00

**p<0.001**

*(MC, HCl, T24, T72)*

0 25 50 75 100

**Time (day)**

0.00

**p<0.001**

*(HCl, T72)*

0 25 50 75 100

**Time (day)**

0.00

**p<0.001**

*(MH, HCl−P60, T24, T49, T72)*

0 25 50 75 100

**Time (day)**

0.00

**p<0.001**

*(T24, T49, T55, T72, combiC, combiH)*

0 25 50 75 100

**Time (day)**

0.00

0 25 50 75 100

**Time (day)**

1.00

***Trifolium pratense***

**#**

**#**

**# #**

1.00

***Trifolium repens***

**#**

**#**

1.00

***Tuberaria guttata***

**#** 1.00

***Urtica dioica***

1.00

***Urtica urens***

0.75

**Probability of not germinating**

0.75

**#** 0.75

**# #**

**#**

0.75

**#**

0.75

**#**

**# # #**

**#**

**#**

**# #**

**p<0.001** *(MC, MH, HCl, HCl−P15,*

*T49, T55, combiC, combiH)*

0.50

0.50

0.50

0.50

0.50

**#**

**Treatments #**

control T24

0.25

MS MC MH

HCl

T49

T55

T72

combiC

0.25

0.25

0.25

0.25

**p<0.001**

HCl−P15 combiH HCl−P60

**p<0.001**

*(HCl−P15, HCl−P60, T24, T49,*

**p<0.001**

**p<0.001**

0.00

*(T49, T55, combiC, combiH)*

0 25 50 75 100

**Time (day)**

0.00

*T55, T72, combiC, combiH)*

0 25 50 75 100

**Time (day)**

0.00

*(T49)*

0 25 50 75 100

**Time (day)**

0.00

*(T55)*

0 25 50 75 100

**Time (day)**

0.00

0 25 50 75 100

**Time (day)**

**Fig. 1.** Probability of not germinating (Kaplan–Meier estimates) of germination functions by species. Treatment curves which differ significantly from the control treatment after applying AFT-models are indicated with # and are listed in the graphs.

**Table 2.** Average values and standard errors for germinability (%) by treatment and species. Different letters on the same row indicate significant differences between treatments within one species (one-way ANOVA and Tukey HSD tests). Different letters in the species column indicate either significant differences between species within each plant family (lower-case letters) or plant families (upper-case letters) for the untreated seed lot. Annual species are underlined. Bold values in the treatment columns indicate significant differences from the control seed lot.

*Cistus albidus* **a**

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Species | Control | MS | MC | MH | HCl | HCl-P15 | HCl-P60 |
| Cistaceae **A** |  |  |  |  |  |  |  |
| *Helianthemum nummularium* **ab** | 23.2 ± 3.0a  13.3 ± 2.4a | **34.8** ± **3.5b**  **24.0** ± **3.3b** | 24.4 ± 1.5ab  5.6 ± 1.7a | 6.9 ± 0.7a | 26.0 ± 1.3ab  7.8 ± 1.0a | 10.7 ± 5.7a | 24.0 ± 3.2a  5.2 ± 1.7a |
| *Tuberaria guttata* **b**  Cyperaceae **BC** | 9.0 ± 3.7ab |  | 8.0 ± 3.5ab | 3.5 ± 0.7a | 20.7 ± 3.5b | 7.3 ± 3.7ab |  |
| *Carex acuta* **a** | 42.0 ± 2.4a | 44.0 ± 3.6a | 40.0 ± 3.6a |  | 39.2 ± 3.8a |  | 29.6 ± 4.3a |
| *Carex ﬂacca* **b** | 70.8 ± 10.3a | 83.2 ± 2.7a | 87.2 ± 3.3a |  | 82.0 ± 2.8a |  | 89.6 ± 3.0a |

Fabaceae **BD**

*Medicago arabica* **a** 13.6 ± 2.6a **81.2** ± **5.1b** 16.8 ± 2.6a 28.0 ± 5.3a *Medicago lupulina* **b** 89.2 ± 1.5ab 91.2 ± 1.7a 93.6 ± 1.8a 92.4 ± 1.7a 89.6 ± 3a  *Trifolium arvense* **b** 83.8 ± 1.9ab 90.8 ± 1.4a 82.3 ± 2.2ab 77.1 ± 0.0b 80.3 ± 2.4b 78.0 ± 5.3b 83.2 ± 1.0ab  *Trifolium campestre* **c** 38.2 ± 2.5a 27.4 ± 2.4ab 26.0 ± 5.0ab 39.3 ± 4.7a 44.7 ± 3.3a

*Trifolium pratense* **d** 60.4 ± 5.5a 52.0 ± 4.2ab 50.7 ± 2.5ab 61.3 ± 1.8a 69.3 ± 13.8a

*Trifolium repens* **b** 86.5 ± 1.1a 86.8 ± 3.7a 83.4 ± 2.2ab 90.7 ± 1.3a 81.3 ± 2.8ab 78.7 ± 7.4ab **73.6** ± **2.6b**

Poaceae **D**

*Po a annua* **a** 96.2 ± 0.8ab 97.6 ± 0.7a 97.5 ± 0.7a 99.3 ± 0.7a 97.5 ± 0.9a 98.0 ± 1.2a 97.6 ± 1.6a

*Poa pratensis* **b** 62.4 ± 3.7ab 63.6 ± 2.7ab 67.8 ± 1.5ab 75.3 ± 1.8ab 67.0 ± 2.3ab 65.3 ± 2.4ab 76.4 ± 5.6a Urticaceae **AC**

*Urtica dioica* **a** 52.1 ± 3.6a 52.4 ± 10.9a 63.5 ± 10.0a 63.5 ± 8.5a 46.9 ± 5.9a

*Urtica urens* **b** 26.0 ± 6.0a **54.0** ± **2.3bc** 50.7 ± 5.4ab **76.9** ± **4.6d 58.0** ± **5.2bcd**

Species T24 T49 T55 T72 combiC combiH

Cistaceae **A**

*Cistus albidus* **a 6.4** ± **1.7c 3.2** ± **0.5c**

*Helianthemum nummularium* **ab** 3.6 ± 1.3a 5.3 ± 1.3a 7.0 ± 2.1a 4.0 ± 1.4a 6.1 ± 3.1a 6.0 ± 3.1a

*Tuberaria guttata* **b** 0.7 ± 0.7a 5.3 ± 3.5a 6.0 ± 4.2ab 7.4 ± 1.3ab

Cyperaceae **BC**

*Carex acuta* **a** 43.7 ± 4.2a 43.6 ± 5.8a

*Carex ﬂacca* **b** 71.9 ± 10.0a 88.4 ± 2.0a Fabaceae **BD**

*Medicago arabica* **a** 14.4 ± 1.6a 18.7 ± 3.4a

*Medicago lupulina* **b** 74.8 ± 3.9b **0.8** ± **0.5c**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| *Trifolium arvense* **b**  *Trifolium campestre* **c** | **52.0** ± **1.4c** | **3.3** ± **1.8d**  **7.3** ± **2.4b** | **16.0** ± **15.0d**  **13.3** ± **4.1b** | **3.6** ± **1.7d** | **3.3** ± **1.3d**  **13.3** ± **1.3b** | **1.3** ± **0.7d**  **12.0** ± **6.9b** |
| *Trifolium pratense* **d** |  | **5.3** ± **2.4c** | **12.7** ± **2.4bc** |  | **13.3** ± **1.8bc** | **3.3** ± **1.3c** |
| *Trifolium repens* **b** | **50.0** ± **2.5c** | **38.0** ± **6.4 cd** | **33.3** ± **0.7 cd** | **1.6** ± **0.7e** | **37.3** ± **5.8 cd** | **15.3** ± **2.9de** |
| Poaceae **D** |  |  |  |  |  |  |
| *Po a annua* **a** | 95.2 ± 1.0ab | 97.3 ± 1.8a | 92.0 ± 1.2ab | 86.0 ± 2.1b | 96.7 ± 1.8ab | 95.3 ± 2.4ab |
| *Poa pratensis* **b** | 72.8 ± 3.8ab | 55.3 ± 6.8b | 71.3 ± 5.8ab | 55.6 ± 2.6b | 71.3 ± 4.1ab | 54.0 ± 9.5b |
| Urticaceae **AC** |  |  |  |  |  |  |
| *Urtica dioica* **a** |  | 42.7 ± 1.8a | 26.9 ± 7.6a |  | 40.3 ± 9.2a | 48.7 ± 4.8a |
| *Urtica urens* **b** |  | **74.5** ± **4.7 cd** | **64.7** ± **1.8bcd** |  | **57.7** ± **1.4bcd** | **75.3** ± **4.7d** |

Survival after endozoochory has been especially correlated with persistent, small, rounded diaspores with a hard seed coat ([Albert](#_bookmark13) [et al.](#_bookmark13) [2015).](#_bookmark13) Hardseededness, a specific type of physical seed dormancy, is a widespread trait in flowering plants. Cistaceae species are characterized by their hard and water impermeable seed coats and do not germinate easily ([Thanos](#_bookmark47) [et al.](#_bookmark47) [1992).](#_bookmark47) Mechanical scarification of the hard seed coat is a well-known practice to induce germination, along

with thermal pre-treatment of the seeds ([Delgado,](#_bookmark16) [Serrano,](#_bookmark16) [López,](#_bookmark16) [&](#_bookmark16) [Acosta](#_bookmark16) [2008,](#_bookmark16) [2001;](#_bookmark16) [Pérez-García](#_bookmark16) [&](#_bookmark16) [González-](#_bookmark16) Benito [2006;](#_bookmark16) [Tavsanoglu](#_bookmark16) [&](#_bookmark16) [Catav](#_bookmark16) [2012).](#_bookmark16) But even if the small and hard seeds of Cistaceae are softened by fire or scarification, the germination rate often remains low. Never- theless, species with dormant seeds are able to escape from crowding or sibling competition by spreading their germina- tion over several seasons ([Russi,](#_bookmark43) [Cocks,](#_bookmark43) [&](#_bookmark43) [Roberts](#_bookmark43) [1992).](#_bookmark43)

This is especially a benefit in the summer-dry and fire-prone Mediterranean climate zone which coincides with the dis- tribution of most Cistaceae species ([Thanos](#_bookmark47) [et al.](#_bookmark47) [1992).](#_bookmark47) Another link has been made between physical dormancy and animal mediated dispersal. When seeds are ingested by herbi- vores water-impermeable seeds are more likely to survive the digestive tract ([Gardener](#_bookmark26) [et al.](#_bookmark26) [1993b)](#_bookmark26) and it has been pointed out that in an evolutionary context, dormancy increases with increasing dispersal while seed size decreases ([Venable](#_bookmark48) [&](#_bookmark48) [Brown](#_bookmark48) [1988).](#_bookmark48) In our experiment, the mechanical scarifica- tion of the seed coat of *C. albidus* and *H. nummularium* increased germinability and germination rate, which is in line with the findings of [Pérez-García](#_bookmark33) [&](#_bookmark33) [González-Benito](#_bookmark33) [(2006).](#_bookmark33) Thermal treatments and chemical treatments using sulphuric acid were also applied by [Pérez-García](#_bookmark33) [&](#_bookmark33) [González-Benito](#_bookmark33) [(2006),](#_bookmark33) but did not lead to conclusive results although there was a general trend towards lower germination following these treatments, which is supported by our results for all tested Cistaceae species. The poor response of these species to our thermal treatments is remarkable as species in this family are known to benefit from high temperatures and even fire ([Delgado](#_bookmark16) [et al.](#_bookmark16) [2001;](#_bookmark16) [Delgado](#_bookmark16) [et al.](#_bookmark16) [2008;](#_bookmark16) [Tavsanoglu](#_bookmark16)

[&](#_bookmark16) [Catav](#_bookmark16) [2012).](#_bookmark16) In Germany, the germination of *H. nummu- larium*, which under natural conditions usually takes place in autumn, was even accelerated towards spring after a con- trolled fire experiment during spring ([Poschlod,](#_bookmark36) [Hoffmann,](#_bookmark36) [&](#_bookmark36) [Bernhardt-Römermann](#_bookmark36) [2011).](#_bookmark36) On the other hand, our ther- mal treatments simulating the wet and warm environment in herbivore guts can hardly be compared with the hot and dry environment characteristic for fires, and the tempera- tures were presumably not high enough to damage the seed coat. We should also keep in mind that the experimental period of 100 days might be rather short for slow germinat- ing species. A viability test on the ungerminated seeds would have allowed us to differentiate between dead and dormant seeds.

Another family characterized by physical dormancy caused by a water impermeable seed coat are the Fabaceae. [Gresta,](#_bookmark32) [Avola,](#_bookmark32) [Anastasi,](#_bookmark32) [and](#_bookmark32) [Miano](#_bookmark32) [(2007)](#_bookmark32) even concluded that mature seeds of *M. arabica* and *M. lupulina* always have impermeable seed coats. The germinating seeds in our con- trol treatment might indicate that physical dormancy was not yet established in some of the *Medicago* seeds. Physical dormancy also occurs in *Trifolium* species. In a germination experiment using seeds of wild populations of *T. repens*, up to 35% of all viable seeds proved to be water-impermeable at maturity ([D’hondt,](#_bookmark11) [Brys,](#_bookmark11) [&](#_bookmark11) [Hoffmann](#_bookmark11) [2010).](#_bookmark11) In our exper- iment, the germination of *M. arabica* was stimulated after mechanical scarification with sandpaper, while this treatment had no significant effect on any other species in the legume family. The chemical, thermal and combination treatments rather had a negative effect on germination which suggests that gut passage results in viable seed loss. Similar experi- ments simulating digestion by sheep ([Peco,](#_bookmark32) [López-Merino,](#_bookmark32)

[&](#_bookmark32) [Alvir](#_bookmark32) [2006)](#_bookmark32) or cattle ([Gardener](#_bookmark26) [et al.](#_bookmark26) [1993b)](#_bookmark26) indeed found a lower germinability of Mediterranean grassland species and

higher survival percentage of hard-seeded legumes compared to soft-seeded species. In our experiment, the duration of the thermal treatment and germinability of legume species were negatively correlated. However, other factors may be causing these results. After 10–14 days, the major part of the ungerminated legume seeds started to show symptoms of fungal and bacterial infections characterized by green, black or white hyphae or pink slime, whereas few seeds of other species were infected. These infections were most probably initiated during the thermal treatment after which most of the seeds were clearly swollen. Imbibition is the first step in seed germination, but it also makes the embryo and cotyledons susceptible to pathogens ([Baskin](#_bookmark14) [&](#_bookmark14) [Baskin](#_bookmark14) [2001).](#_bookmark14)

Nevertheless, many Cistaceae and Fabaceae species were found in dung and their germination often was proved to be higher after gut passage. Goat feeding experiments resulted in the retrieval of high numbers of *C. albidus* seeds ([Grande](#_bookmark29) [et al.](#_bookmark29) [2013)](#_bookmark29) and even increased germination of *Cistus salvifolius* ([Mancilla-Leyton](#_bookmark45) [et al.](#_bookmark45) [2011).](#_bookmark45) Furthermore, the germina- tion of six Mediterranean Cistaceae species increased up to seven-fold after a feeding experiment with sheep ([Ramos](#_bookmark38) [et al.](#_bookmark38) [2006).](#_bookmark38) On the other hand, in a feeding experiment using sheep, cattle, rabbits, horses and donkeys the germi- nation success was lower for *H. nummularium*, *Trifolium arvense*, *Trifolium campestre*, *Trifolium pratense* and *T. repens* ([Cosyns,](#_bookmark8) [Delporte,](#_bookmark8) [et al.](#_bookmark8) [2005),](#_bookmark8) whereas a simi- lar experiment using cattle ([D’hondt](#_bookmark12) [et al.](#_bookmark12) [2011)](#_bookmark12) achieved higher germinability of *H. nummularium* and *T. pratense* seeds. *U. dioica* is known to germinate abundantly from dung ([Pakeman](#_bookmark31) [et al.](#_bookmark31) [2002;](#_bookmark31) [Cosyns,](#_bookmark31) [Claerbout,](#_bookmark31) [et al.](#_bookmark31) [2005;](#_bookmark31) [Cosyns](#_bookmark31) [&](#_bookmark31) [Hoffmann](#_bookmark31) [2005;](#_bookmark31) [Couvreur](#_bookmark10) [et al.](#_bookmark10) [2005)](#_bookmark10) and, in our experiments, germination was not impaired by any of the treatments, indicating that this species indeed is well- adapted to endozoochorical dispersal. More interestingly, treated seeds of the congeneric species *U. urens* germinated significantly better and faster compared to the control seed lot, which suggests that this species is able to benefit twice from endozoochory: once by the dispersal movement itself and additionally by an increased germination success at the deposition site. However, despite this high germination suc- cess *U. urens* has been rarely found germinating in dung and when found, few individuals emerge from dung ([Malo](#_bookmark44) [&](#_bookmark44) [Suarez](#_bookmark44) [1996).](#_bookmark44)

Our treatments had a very limited effect on the germinabil- ity of the tested *Carex* and *Poa* species, which conflicts with other studies where germination was negatively affected by gut passage ([Cosyns,](#_bookmark8) [Delporte,](#_bookmark8) [et al.](#_bookmark8) [2005;](#_bookmark8) [D’hondt](#_bookmark12) [et al.](#_bookmark12) [2011).](#_bookmark12) The time ratio even indicates that germination of *Poa pratensis* and *C. ﬂacca* is accelerated after chemical treatment with hydrochloric acid, which is also supported by the results of [Salehi](#_bookmark44) [and](#_bookmark44) [Khosh-Khui](#_bookmark44) [(2005)](#_bookmark44) who achieved a higher ger- minability and germination rate of *P. pratensis* after bathing the seeds in sulphuric acid. While it is commonly known that these species are successfully dispersed by endozoo- chory (e.g., [Pakeman](#_bookmark31) [et al.](#_bookmark31) [2002;](#_bookmark31) [Cosyns,](#_bookmark31) [Claerbout,](#_bookmark31) [et al.](#_bookmark31) [2005;](#_bookmark31) [Couvreur](#_bookmark10) [et al.](#_bookmark10) [2005;](#_bookmark10) [Cosyns](#_bookmark10) [et al.](#_bookmark10) [2006),](#_bookmark10) we should

also keep in mind that we as well as [Salehi](#_bookmark44) [and](#_bookmark44) [Khosh-Khui](#_bookmark44) [(2005)](#_bookmark44) did not simulate all steps of the digestive tract, while the other studies used true gut passage to test germination effect. We simulated the effects of the acid environment in the stomach and duodenum and the effect of a proteolytic enzyme (pepsin) in combination with an acid, whereas the amylolytic and lipolytic enzymes produced in the digestive system and the proteolytic and cellulolytic enzymes secreted by bacteria were left out in this experiment. Although the endozoochorous dispersal of plant seeds is correlated with diaspore size, shape, seed coat morphology, seed longevity and seed production, ungulate traits (e.g., habitat use, diet and digestive system) are at least as important in determin- ing whether a plant species is an endozoochorous disperser ([Albert](#_bookmark13) [et al.](#_bookmark13) [2015).](#_bookmark13)

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