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The effect of seed morphology on the potential dispersal of aquatic macrophytes by the common carp (*Cyprinus carpio*)

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SUMMARY

1. The potential for seed dispersal by fish (ichthyochory) will vary among aquatic plants because of differences in seed size and morphology.
2. To examine how seed morphology influences the probability of dispersal by the common carp (*Cyprinus carpio*), we studied seed ingestion, retention time and subsequent egestion and germination of seeds of *Sparganium emersum* and *Sagittaria sagittifolia*, two aquatic plant species with similar sized but morphologically different seeds.
3. We compared dispersal probabilities between the two plant species, in which the probability of dispersal is assumed to be a function of the probabilities of seed ingestion, egestion and germination, and the dispersal distance is assumed to be a function of seed egestion rate over time.
4. We found that, although the soft seeds of *S. sagittifolia* had an approximately 1.5 times higher probability of being ingested by the carp than the hard seeds of *S. emersum* (83.15% ± 1.8% versus 56.16% ± 2.7%, respectively), the latter had an almost twofold higher probability of surviving the passage through the digestive tract (38.58% ± 2.7% versus 20.97% ± 1.5%, respectively). Patterns of seed egestion over time did not differ between the two plant species, despite the difference in seed morphology. Gut passage had a different effect on seed germination between plant species. Compared with non-ingested controls, seeds of *S. emersum* showed a 12.6% increase in germination and a 2.1 day acceleration in germination rate, whereas seeds of *S. sagittifolia* displayed a 47.3% decrease and 5.1 day delay, respectively.
5. Our results suggest that seed morphology affects the dispersal probability and postdispersal establishment, but not the dispersal distance, of aquatic plants that are dispersed by fish.

Keywords: endozoochory, gut passage, ichthyochory, postdispersal establishment, retention time

Introduction

Animal-assisted transport of propagules has long been considered an important mode of plant dispersal in aquatic environments (Darwin, 1859; Ridley, 1930). Waterbirds and fish are among the most likely candidates to play a role in the zoochorous dispersal of aquatic plants (Cook, 1988; Barrat-Segretain, 1996).

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While seed dispersal by waterfowl has received considerable attention (e.g. Clausen *et al.*, 2002; Figuerola, Green & Santamaría, 2002; Charalambidou, Santamaría & Langevoord, 2003; Charalambidou *et al.*, 2005; Pollux, Santamaría & Ouborg, 2005), seed dispersal by fish has not been studied systematically. Although circumstantial, there are a number of findings that indicate that seed dispersal by fish (i.e. ichthyochory) may be important. Firstly, stomach-content analyses on temperate European and North American fishes show the presence of seeds in many different species (Ridley, 1930; Crivelli, 1981; Bergers, 1991; García-Berthou, 2001; Chick, Cosgriff & Gittinger, 2003; Nurminen *et al.*, 2003; M.C. Van Riel, unpubl. data). Furthermore, on average, 1–5% of the field-collected individuals of these species bear seeds in their stomachs (Bergers, 1991; M.C. Van Riel, unpubl. data). Occasionally, seeds are found in a much larger proportion of the fish population; e.g. 73–78% of the channel catfish (*Ictalurus punctatus*, Rafinesque) from the Mississippi River (U.S.A.), and 42–93% of the common carp (*Cyprinus carpio*, L.) from Lake Banyoles and the Carmargue (Spain and France, respectively; Crivelli, 1981; García-Berthou, 2001; Chick *et al.*, 2003). Moreover, observed seed quantities in the stomachs of individual fish range from a few to more than a 1000 seeds per stomach (Ridley, 1930; Crivelli, 1981; Bergers, 1991; Chick *et al.*, 2003; Nurminen *et al.*, 2003). Combining the prevalence of seeds in fish stomachs with the fact that many lake and river systems may harbour high numbers of fish (easily reaching several hundreds of thousands; e.g. Van Densen, Steinmetz & Hughes, 1990), suggests that, collectively, fish may play an important role in the dispersal of temperate and aquatic riparian plants.

However, little is known about the role of seed morphology on seed ingestion during fish feeding, although this factor may determine which plant species are actually dispersed. Furthermore, from studies using various terrestrial animal models we know that passage rates, the proportion of seeds egested and the germination potential of ingested seeds are influenced by the size and morphology of the seeds (Traveset, 1998), although this has rarely been investigated in fish (Agami & Waisel, 1988; Smits, van Ruremonde & van der Velde, 1989; Traveset, 1998). The purpose of this study was to determine whether aquatic plants with different seed structures differ in their potential for ichthyochoric dispersal. Using common carp (*C. carpio*) we compared the ingestion, retention time and subsequent egestion and germination of seeds of unbranched bur-reed (*Sparganium emersum* Rehmann 1872, Sparganiaceae) and arrowhead (*Sagittaria sagittifolia* Linnaeus 1753, Alismataceae). We used a modelling approach for comparing dispersal probabilities between the two plant species, in which (i) the probability of dispersal is assumed to be a function of the probabilities of seed ingestion, retrieval and germination and (ii) the dispersal distance is assumed to be a function of the retrieval rate over time. We hypothesised that *S. emersum* would show a lower probability of ingestion, but a higher probability of retrieval and germinability, owing to the hard scleridial seed coat, as compared with the soft seed coat of *S. sagittifolia*.

Methods

Study species

The common carp *C. carpio* is one of the most widely spread freshwater fish species, commonly found in lakes, canals and lowland rivers in temperate and tropical regions of Eurasia and North America. Dietary studies on field-collected individuals have shown that *C. carpio* is an opportunistic omnivorous forager, that includes macrophyte seeds in its diet (Ridley, 1930; Crivelli, 1981; Bergers, 1991; García-Berthou, 2001). *Sparganium emersum* and *S. sagittifolia* are helophyte plant species that are also widely distributed along canals and lowland streams throughout Eurasia and North America (Cook & Nicholls, 1986). The seeds of the two species are similar in size, but differ greatly in their morphology. The drupe-like fruit of *S. emersum* consists of a seed enclosed in a hard scleridial endocarp and a tough spongy mesocarp, with a plugged pointy micropyle (Cook & Nicholls, 1986). The fruit of *S. sagittifolia* consists of a nutlet-like seed surrounded by a soft membranous endocarp and a fleshy, semi-transparent, laterally compressed disc-like mesocarp. The common carp (*C. carpio*) and the two plant species (*S. emersum* and *S. sagittifolia*) overlap in their distribution and it has been suggested that seeds of both plant species may be dispersed by carp (Hochreutiner, 1899; reference taken from Ridley, 1930).

Experimental design

Ripe seeds of *S. emersum* and *S. sagittifolia* were collected during October 2003 from natural populations in the Netherlands. The seeds of both species need to be cold-stratified (i.e. subjected to cold temperature for an extended period) while being immersed in water, to break seed dormancy (Muenscher, 1936). Therefore, the seeds were stored in glass jars filled with tap water, in a dark cold room at 5 ± 1 °C, to mimic natural conditions of Central-North European winters.

Twelve common carp with a mean mass of 0.307 ± 0.01 kg (SE) were obtained from Ruud Vonk Fish Hatchery (Maurik, the Netherlands) in October 2003. The fish were individually kept in 100-L tanks in the fish facilities of Radboud University Nijmegen, the Netherlands and fed daily on a fixed diet of commercial pellets (Trouvit; Trouw & Co, Putten, the Netherlands) amounting to 1% of their body mass. The water in the tanks was maintained at 24 °C and was continuously aerated and refreshed (50 L h^{-1}). To ensure homogenisation of water quality among the twelve tanks, all were supplied with water coming from the same filtering system.

From January to April 2004, we performed 12 feeding trials at weekly intervals. At the beginning of a feeding trial, each of the twelve fish was fed a total of 10 Trouvit food pellets (each pellet containing five randomly selected *S. emersum* and five *S. sagittifolia* seeds). Five to 10 min after feeding, non-ingested seeds (i.e. seeds that were expelled by 'spitting'; Sibbing, Osse & Terlouw, 1986) were removed from the tanks with aquarium nets (frame size 10 × 15 cm; mesh size 1 mm) and counted. Fish faeces were then collected every 2 h from the bottom of the tanks by means of aquarium nets for a period of 24 h (preliminary tests, lasting 48 h, showed that the fish always egested all non-digested seeds well within 24 h). Collected faeces were immediately rinsed with tap water and sieved using a 500 μm square mesh size sieve (diameter 19 cm). Seeds retrieved were transferred to plastic containers (100 mL) filled with tap water and returned to the dark cold room (5 ± 1 °C) for the remainder of the experiment to ensure an equal cold-stratification period for all seeds in all feeding trials (from seed collection in the field in October 2003 to the germination test in May 2004). For each plant species, three batches of 50 randomly selected non-ingested seeds, were used as controls in the germination experiment. These control seeds received a similar pre- and post-experimental treatment as the seeds used in the feeding experiments (i.e. placed in soft pellets soaked in water, sieved with tap water and stored at 5 ± 1 °C for the remainder of the feeding experiments) to exclude possible effects of pre- or post-feeding treatment of the seeds.

In May 2004, all the egested and control seeds were set to germinate simultaneously in a climate chamber with a photoperiod of 16 L/8 D (light/dark), a daytime irradiance of 200 μmol photons s^{-1} m^{-2} and a day/night temperature cycle of 25/18 °C. Seeds were placed in transparent polystyrene microtiterplates (127 × 82 cm, 96 wells; Omnilabo International BV, Breda, the Netherlands), filled with tap water (one seed per well). Germination, defined as the emergence of the first foliage leaf, was checked daily for a period of 45 days.

Statistical analysis

Differences in total seed ingestion (i.e. proportion of offered seeds that were ingested) and total retrieval (i.e. proportion of ingested seeds recovered from the faeces) were tested by means of General Linear Modelling using the MIXED module for repeated measures in SAS 9.1.2 (Littell, Henry & Ammerman, 1998; SAS Institute Inc, Cary, NC, U.S.A.). Data were arcsine transformed to assure homoscedasticity and the normality of residuals. In the analyses, plant species was added as a fixed factor and feeding trial and fish individual as random factors. Variation between plant species in seed retrieval over retention time was also analysed by means of repeated-measures ANOVA, with retention time added as an additional fixed factor (Charalambidou *et al.*, 2003). To remove the effect of total retrieval from this analysis, data were standardised by dividing data from each retrieval event (i.e. as measured at each retention time interval) by the total retrieval measured in that individual fish. The effect of plant species and seed treatment (i.e. control versus fish-ingested) on total germination (i.e. proportion of seeds that germinated by the end of the germination run), were tested using repeated-measures ANOVA, with plant species added as a fixed factor and feeding trial and fish individual as random factors, followed by pairwise *post hoc* tests comparing the different treatments within each plant species (with a $P < 0.025$ comparisonwise error rate, after Bonferroni correction). Differences in germination rate were tested in a survival analysis by fitting a Cox proportional hazards regression to the number of days between setting for germination and seedling emergence, for each individual seed that germinated, using S-Plus 2000 (Mathsoft Engineering and Education Inc., Zoetermeer, the Netherlands). To separate the effects of germination rate from those of total germination, non-germinated seeds were excluded from the analysis. For each plant species we fitted separate models, with seed treatment as a fixed factor and individual (for fish-ingested) or batch replicate (for controls), respectively, as a random (or frailty) effect.

Results

All food pellets with seeds offered to the carp were eaten, i.e. they were taken into the oral cavity where they were 'chewed upon' (i.e. process of oral examination of food; Sibbing *et al.*, 1986). Shortly afterwards, items that were apparently unpalatable were expelled by means of 'spitting'. Only seeds were expelled, the rest of the food pellets was always (re-) ingested. The results revealed a significant difference in total seed ingestion (i.e. the proportion of ingested seeds over seeds offered) between the two plant species ($F_{1,275} = 21.65$, $P < 0.0001$). The hard, pointed seeds of *S. emersum* had a significantly lower ingestion of 56.16% ± 2.7% (SE), compared with the softer *S. sagittifolia* seeds with 83.15% ± 1.8% being ingested (Fig. 1a).

The total retrieval (i.e. the proportion of retrieved seeds after egestion over seeds ingested) differed significantly between the two plant species ($F_{1,268} = 13.44$, $P = 0.0003$), being higher for *S. emersum* (38.58% ± 2.7%) than in *S. sagittifolia* (20.97% ± 1.5%; Fig. 1b). As the fish faeces contained many seed fragments, especially during the first 10 h, the rest of the ingested seeds were probably digested. The pattern of seed retrieval over time followed a leptokurtic curve which was indistinguishable for the two plant species ($F_{1,11} < 0.001$, $P = 0.9979$; Fig. 2). For both species, maximum seed retrieval was observed at 8 h, and the last seeds were found in the faeces after 18 h (for *S. sagittifolia*) to 20 h (*S. emersum*) after ingestion.

Seed germination (i.e. the total proportion of germinated seeds over retrieved seeds) was higher

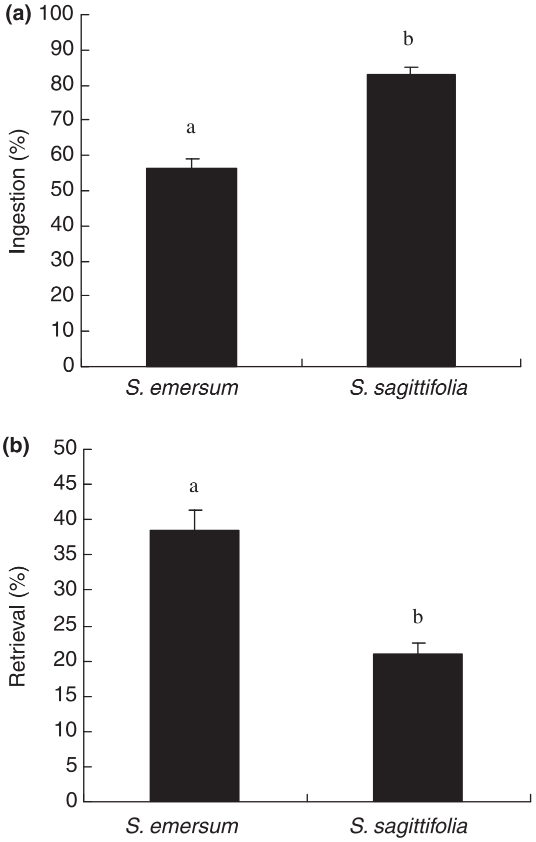

Fig. 1 (a) Mean (±SE) seed ingestion (%) and (b) seed retrieval (%) over 24 h, of *S. emersum* and *S. sagittifolia* seeds fed to carp ($n = 12$ feeding trials, each trial with $n = 12$ fish). Bars that do not share a common letter are significantly different from each other (see text for P-values).

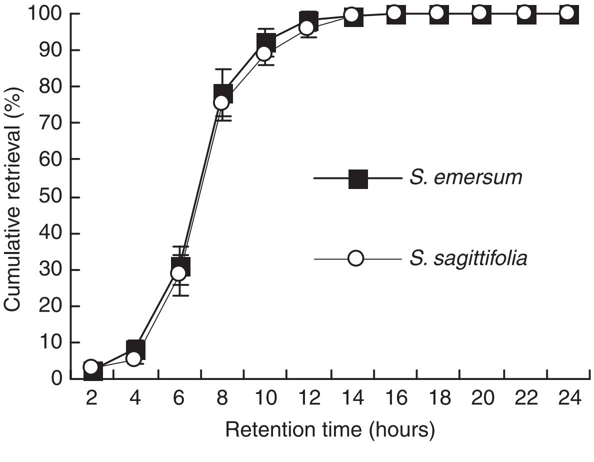

Fig. 2 Mean (±SE) cumulative retrieval (%) [(number of seeds egested after n hours after ingestion/total number of seeds egested) × 100] for *S. emersum* and *S. sagittifolia* seeds ingested by carp ($n = 12$ feeding trials, each trial with $n = 12$ fish).

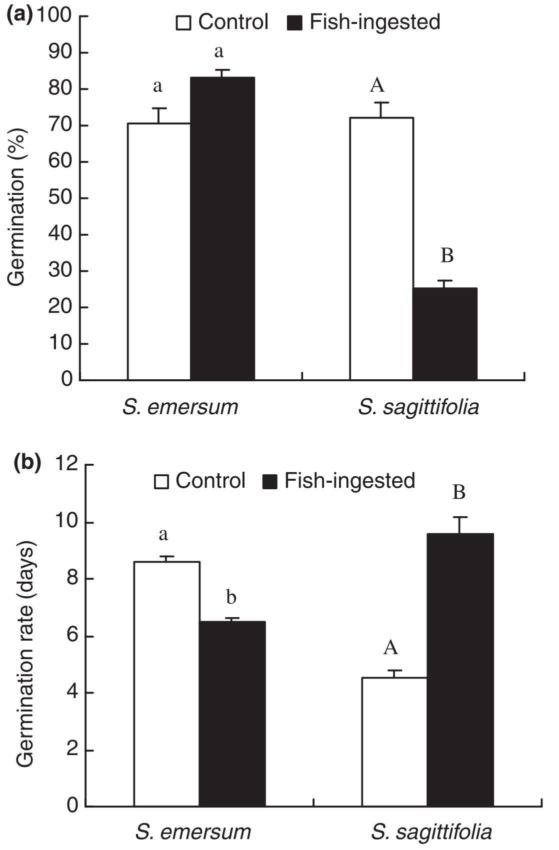

Fig. 3 (a) Mean (±SE) seed germination (%) and (b) germination rate (number of days to germination) of non-ingested control (n = 150, in three batches of 50 seeds) and fish-ingested (n = 12 feeding trials, each trial with n = 12 fish) seeds of *S. emersum* and *S. sagittifolia*. For each species, significant differences between control and fish-ingested seeds were indicated with letters (a and b for *S. emersum* and A and B for *S. sagittifolia*). Bars that do not share a common letter are significantly different from each other (see text for P-values).

for *S. emersum* than for *S. sagittifolia* ($F_{1,226} = 461.24$, $P < 0.0001$; Fig. 3a). For *S. emersum*, germination of non-ingested control seeds (70.67% ± 4.1%) did not differ significantly from fish-ingested seeds (83.27% ± 2.2%; $F_1 = 1.30$, $P = 0.2569$), while for *S. sagittifolia*, control seeds showed a significantly higher total germination than fish-ingested seeds (72.33% ± 3.8% and 25.04% ± 2.3%, respectively; $F_1 = 6.54$, $P = 0.012$; Fig. 3a). Control seeds of *S. emersum* did, however, display a slower germination rate (i.e. number of days to germination) compared with fish-ingested seeds (Cox regression: $\chi^2 = 39.1$, d.f. = 1, $P < 0.001$), as opposed to *S. sagittifolia*, where control seeds displayed significantly faster germination rates compared with fish-ingested seeds (Cox regression: $\chi^2 = 36.4$, d.f. = 1, $P < 0.001$; Fig. 3b).

Discussion

Ingestion

Analyses of the stomach contents of fish caught in the field show that temperate species, particularly cyprinids such as *C. carpio*, ingest seeds as part of their diet (Crivelli, 1981; Bergers, 1991; García-Berthou, 2001; Nurminen *et al.*, 2003). Little is known about which plant species are ingested, however, or whether certain seed structures might affect the probability of ingestion. This study shows that under controlled conditions the soft seeds of *S. sagittifolia* are 1.5 times more likely to be ingested than the hard seeds of *S. emersum*. Several studies have reported highly complex food selection mechanisms in temperate cyprinids, involving morphological and behavioural adaptations as well as mechanical and chemical senses, for the detection and investigation of potential food items (Sibbing *et al.*, 1986; Sibbing, 1988; Callan & Sanderson, 2003). For many temperate cyprinids these mechanisms are crucial as they take up their food along with unpalatable debris (e.g. detritus, sand and stones). In the oral cavity, palatable and unpalatable items are separated and the unpalatable particles expelled by 'spitting' (a reversed suction pump action of the orobuccal and opercular cavities; Sibbing *et al.*, 1986; Callan & Sanderson, 2003). Our results show that the hard, pointed, drupe-like seeds of *S. emersum* are more likely to be identified as unpalatable items and expelled by carp than the soft, fleshy, disc-like seeds of *S. sagittifolia* and thus that seed characteristics are likely to affect seed ingestion by fishes.

Retention time and total retrieval

We found no difference in seed retention time in the digestive tract of carp between *S. emersum* and *S. sagittifolia*. However, this outcome is consistent with studies examining the effect of food type on the gastric evacuation rate of fish (i.e. the time required to evacuate the stomach content). These studies used a wide variety of invertebrate prey species, often with large differences in size, carapace hardness and biochemical composition, and yet reported little difference in the evacuation rates (Persson, 1979, 1982; Brodeur, 1984; Nilsson & Brönmark, 2000). Therefore, we suggest that in animals with a relatively unspecialised gut morphology, such as fish, seed morphology does not affect seed retention time (this study), as opposed to animals with a highly specialised gut morphology, such as waterfowl, where seed morphology significantly affects seed retention times (Pollux *et al.*, 2005).

Furthermore, seed survival during gut passage is known to depend on a complex interaction between the characteristics of the seeds and of the animal consumers (Traveset, 1998; Charalambidou & Santamaría, 2002). For instance, in large mammalian herbivores (sheep, cattle and horses) small-seeded species tend to survive better than large-seeded species, probably because the latter sustain more mechanical damage by chewing (Pakeman, Digneffe & Small, 2002; Mouissie *et al.*, 2005). However, in animals that lack this initial mechanical chewing stage, e.g. waterfowl, the hardness of the seed coat appears to be more important than seed size (Proctor, 1968; Charalambidou & Santamaría, 2002; Pollux *et al.*, 2005). Our study suggests that also in fish, seed coat hardiness is an important factor for seed survival, with the harder seeds of *S. emersum* having an almost twofold higher probability of retrieval compared with *S. sagittifolia*. This concurs with two studies by Smits *et al.* (1989), who showed that seeds of three nymphaeid waterplants had a lower probability of being egested intact compared with seeds of two (harder-seeded) *Potamogeton* species when fed to carp, and by Agami & Waisel (1988) who retrieved a greater percentage of hard seeds than of the soft seeds of *Najas marina* after ingestion by fish.

Seed viability

Passage through the guts of vertebrate frugivores may affect seed germination (either positively or negatively) by: (i) removal of the fruit's pulp or the germination inhibitors within it and (ii) the mechanical/chemical treatment of the seed coat in the animal's gut (Traveset, 1998). Our study revealed a decreased germination for *S. sagittifolia* and an increased germination for *S. emersum* seeds that passed through the intestinal tract of carp. The reduction in germination and germination rate of the soft *S. sagittifolia* seeds is most likely to be due to the bruising of the seed embryo reducing its capacity to germinate. The increase in germination and germination rate of *S. emersum* seeds is probably related to the breaking of the seed coat dormancy by mechanical abrasion or removal of the seed coat (Baskin & Baskin, 1998), which is necessary before the seeds can germinate (Cook, 1962). Under natural conditions the seed coat dormancy of *S. emersum* can be broken after a period of freezing, or by natural decomposition. Alternatively, seed coat dormancy of hard coated seeds of aquatic plants may be broken by passage through the digestive tract of fishes (Agami & Waisel, 1988; Smits *et al.*, 1989; this study) and waterfowl (Santamaría *et al.*, 2002; Pollux *et al.*, 2005), leading to increased germination.

A simple model for comparing dispersal probabilities between plant species

Seed dispersal by animals is often studied by means of seed feeding-experiments. These studies are designed to estimate a number of parameters, which are used to predict the probability and distance of dispersal. These are (i) the probability of seed ingestion $P(\mathrm{i})$, which yields information on feeding preferences or food selection mechanisms, (ii) the probability of seed retrieval $P(\mathrm{r})$, which yields information about the survival of seeds during gut passage, (iii) seed retention time, which (in combination with information on migration patterns of the animal disperser) yields information about the dispersal curve and potential dispersal distances, (iv) the probability of seed germination $P(\mathrm{g})$ of retrieved seeds, which yields information about the probability of seed establishment after gut passage and (v) germination rate, which yields information about competitive (dis)advantages over non-ingested conspecific seeds, that may arise from an earlier or later onset of germination.

In combination with the relative availability of seeds $P(\mathrm{a})$, this kind of information can be used to compare the dispersal probability of different plant and animal species. In the field the availability of seeds may vary widely, both within species (between different locations) and between species, largely depending on the distribution of the plants and their reproductive output (which in turn may both vary widely across environmental conditions). For the purposes of this study, however, we ensured an equal availability of seeds of both plant species in the food

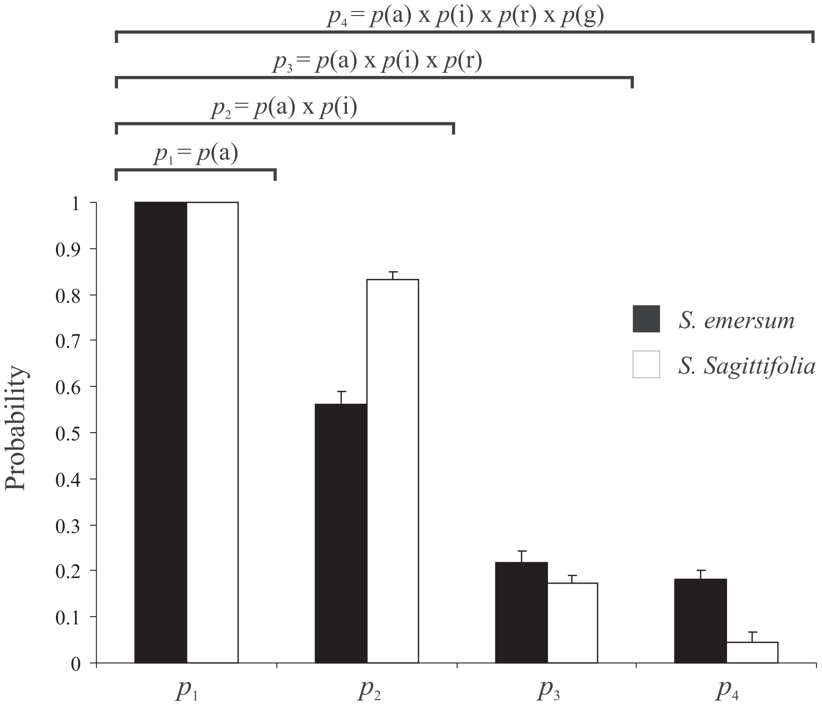

Fig. 4 A simple modelling approach comparing the probability of fish-mediated dispersal of *S. emersum* and *S. sagittifolia*, as derived from four successive steps (see text for explanation). The comparison is based on parameters inferred from the feeding experiments: $P(\mathrm{a}) =$ probability of seed availability [in this study $P(\mathrm{a})$ is equal to 1], $P(\mathrm{i}) =$ probability of ingestion, $P(\mathrm{r}) =$ probability of egestion and $P(\mathrm{g}) =$ probability of germination.

pellets [$P(\mathrm{a}) = 1$]. Under the assumption that both plant species have a similar seed availability to the fish [$P(\mathrm{a}) = 1$], our results show that, although *S. sagittifolia* has a 1.5 times higher probability of being ingested, this initial advantage is nullified by a twofold higher probability of seed egestion in *S. emersum* combined with a three times higher probability of seed germination. The results thus suggest that *S. emersum* has a higher probability [calculated as $P_4 = P(\mathrm{a}) \times P(\mathrm{i}) \times P(\mathrm{r}) \times P(\mathrm{g})$, see Fig. 4) of being dispersed by carp, compared with *S. sagittifolia* ($P =$ 0.1804 and 0.0437, respectively). As there are no significant differences between both plant species in their seed retention times, differences in dispersal distances arising from carp-mediated dispersal would not be predicted. Finally, although there are clear contrasting effects on germination rate (of egested compared with control seeds) between the two plant species (with an increase for *S. emersum* and decrease for *S. sagittifolia*), a recent study by Figuerola *et al.* (2005) has shown that such short time (dis)advantages are not likely to result in de- or increased plant performances over longer time periods. Thus, we must conclude that, based on all the parameters measured in this study, *S. emersum* has: (i) an overall higher potential for carp-mediated dispersal and postdispersal establishment and (ii) an equal dispersal curve, indicating equal dispersal distances arising from carp-mediated dispersal, compared with *S. sagittifolia*.

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