Differences in endozoochorous dispersal between aquatic plant species, with reference to plant population persistence in rivers

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SUMMARY

1. In river ecosystems, populations are continuously subjected to unidirectional downstream currents resulting in a downstream movement of populations. To ensure long-term population persistence in rivers, organisms must have a mechanism for upstream dispersal, which allows them to re-colonise upstream areas.

2. In this study we assessed differences in the potential for endozoochorous seed dispersal of *Sparganium emersum* and *Sagittaria sagittifolia*, two aquatic plant species with different seed morphologies, by mallard (*Anas platyrhynchos*) and teal (*Anas crecca*), two duck species with different body weights.

3. We found no significant differences in seed retrieval (the proportion of ingested seeds retrieved after gut passage) and seed retention time (time between seed ingestion and retrieval), between mallard and teal, despite the difference in body weights. We did find a significantly higher germination (%) over retention time of *S. emersum* seeds retrieved from teal compared with mallard, most likely related to a more efficient removal of the seed coat during passage through the gut of teal.

4. There were large differences between *S. emersum* versus *S. sagittifolia* in: (i) seed retrieval (22.65 ± 20.8% versus 1.60 ± 2.4%, respectively); (ii) seed retention time in duck gut, with a maximum of 60 h versus 12 h; (iii) the effect of gut passage on seed germination, with an increase of approximately 35% versus a decrease of 25%; and (iv) the effect of gut passage on seed germination rate, with an acceleration of 10 days versus a delay of 3 days on average. The results show that *S. emersum* has a higher potential for endozoochorous dispersal by ducks and postdispersal establishment than *S. sagittifolia*.

5. We propose that, in rivers, bird-mediated seed dispersal may promote re-colonisation of upstream areas, enabling long-term plant population persistence.

Keywords: aquatic plants, birds, drift-paradox, population persistence, upstream dispersal, zoochory

Introduction

Rivers and streams are linear habitats that impose special constraints on dispersal and persistence of aquatic organisms (Imbert & Lefèvre, 2003). Populations in rivers are continuously subjected to water currents and, although most species display adaptations that prevent them from being washed away under normal circumstances, in the absence of a mechanism for upstream dispersal, any advection (no matter how small) will ensure that, on average, populations will move downstream, preventing long-term persistence (Speirs & Gurney, 2001). In

addition, during catastrophic and aperiodic floodings whole populations may be washed away to downstream areas (Stelter *et al.*, 1997). Hence, aquatic organisms that have stable and persistent populations in river ecosystems may be expected to display mechanisms for upstream dispersal, either active or passive.

For aquatic invertebrates this problem has received considerable attention, starting with Müller's (1954) concept of 'the colonisation cycle' whereby aquatic insects compensate for the gradual downstream movements of the larvae by actively flying (Müller, 1974; Speirs & Gurney, 2001), swimming or crawling upstream (Humphries & Ruxton, 2002). However, in contrast to aquatic insects, other invertebrate species may display a sessile adult life-style and therefore lack a means of active upstream dispersal. For example, the zebra mussel *Dreissena polymorpha* (Pallas, 1771) has a sessile adult life-style and short-lived, free-swimming larvae with limited swimming capabilities, leading to downstream dispersal in rivers. Despite these difficulties, during the last two centuries zebra mussels have succeeded in colonising all main European rivers because of passive (human-mediated) upstream dispersal (Kinzelbach, 1992; Pollux *et al.*, 2003). Aquatic plants in rivers face similar difficulties, i.e. a sessile adult life-style and passive hydrochorous downstream dispersal of propagules (seeds and plant fragments). This, together with the notion that all over the world aquatic plants can be found in riverine systems, suggests that they must also possess a means of assisted upstream dispersal. Surprisingly, the problem of upstream dispersal for ensuring plant population persistence in river ecosystems has received little attention.

Aquatic plants are generally dispersed by water (Sculthorpe, 1967; Cook, 1988) and in rivers water flow can be considered the main dispersal vector leading to dispersal in the downstream direction (Barrat-Segretain, 1996). In addition, it has been suggested that animals, particularly fishes and water birds, may play a role in the dispersal of aquatic plants (Clausen *et al.*, 2002; Green, Figuerola & Sanchez, 2002). The role of waterbirds in the passive endozoochorous dispersal of seeds was recognised a long time ago (Ridley, 1930 and references therein); however, most evidence for such dispersal was anecdotal and detailed quantitative data were lacking. Since then, few experimental studies have investi-

gated the mechanism or frequency of endozoochorous transport by waterfowl (Charalambidou & Santamaria, 2002; Figuerola & Green, 2002). Based on the information gained to date, Charalambidou & Santamaria (2002) identified several gaps in our knowledge of waterbird dispersal. Among these, comparisons between duck species exhibiting different diets and/or body sizes, and comparisons between plant species with different seed characteristics (e.g. size and morphology) were considered to be of particular interest.

In this study we assessed whether ducks might function as dispersal agents for seeds of two aquatic plant species with different seed morphologies but comparable habitat requirements, unbranched burr-reed *Sparganium emersum* (Rehmann, 1872; Sparganiaceae) and arrowhead *Sagittaria sagittifolia* (Linnaeus, 1753; Alismataceae). In particular, we were interested in whether the two plant species differ in their potential for endozoochorous dispersal by waterfowl, and if these differences could be related to their distribution along river courses. Our specific hypothesis was that *S. emersum* shows a higher potential for endozoochorous seed transport and thus might have a higher capacity for upstream colonisation, owing to the higher resistance to gut passage conferred by a hard scleridial endocarp and tough spongy mesocarp, as compared with the soft membranous endocarp and fleshy mesocarp of *S. sagittifolia* seeds. To test this, we performed a gut passage experiment using captive ducks and contrasted its results with those of a field survey where the distribution of both species along two whole river courses was mapped. As a second question we addressed whether different duck species differ in their capacity for endozoochorous seed dispersal. We hypothesised that differences in morphological and physiological properties of the intestinal tract between duck species lead to differences in the digestion and retention of seeds, and hence to differences in potential for endozoochorous seed dispersal (Charalambidou & Santamaria, 2002).

Material and methods

Study species

S. emersum and *S. sagittifolia* are widely distributed throughout Eurasia and North America (Cook & Nicholls, 1986). In Europe, *S. emersum* and *S. sagittifolia*

display similar habitat requirements and are often found together in an association called Sparganieto–Sagittarietum (Cook & Nicholls, 1986; Riis, Sand-Jensen & Vestergaard, 2000; Burkart, 2001). They are typically found together in canals and streams characterised by shallow, stagnant to slow flowing, nutrient-rich freshwaters with sandy or muddy bottoms. However, in river systems, *S. emersum* generally displays a wider longitudinal distribution compared with *S. sagittifolia*, despite the presence of suitable slow-flowing habitats. 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 micropyle (Cook, 1962, 1996). 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.

Sparganium and *Sagittaria* fruits (hereafter called seeds) are important food for many waterfowl species. To study the potential for endozoochorous seed dispersal of both plant species by waterfowl, we selected mallard *Anas platyrhynchos* (Linnaeus, 1758) and teal *Anas crecca* (Linnaeus, 1758). During fall and winter, the period of seed release and seed dispersal of *S. emersum* and *S. sagittifolia*, they are among the most wide spread waterfowl species in The Netherlands (Voslamber, Van Winden & Van Roomen, 1998; Devos, 2001), using streams and rivers as their winter habitat (Van Noorden, 1992). During this period, their diet consists mainly of seeds and plant fragments of aquatic plants, grasses and sedges, including seeds of *Sparganium* spp. and *Sagittaria* spp. (McAtee, 1918; Metcalf, 1931; Martin & Uhler, 1939; Anderson, 1959; Nummi, 1993; Green *et al.*, 2002; Mueller & Van der Valk, 2002). Moreover, they display local migratory movements within a home range (e.g. diurnal feeding migrations; Guillemain, Houte & Fritz, 2000, 2002; Mack, Clark & Howerter, 2003), potentially allowing for seed dispersal away from the plant populations, along the longitudinal axis of the river.

Site description

The River Rur (catchment surface area of 2340 km^2) originates in the Ardennes Mountains near the Belgian border (at 650 m above sea level (a.s.l.)), flows through Germany (143.5 km) and The Netherlands (21.5 km), where it discharges in the River Meuse (at 16.8 m a.s.l.). The channel width varies

between 20 and 40 m. The seasonal hydrology is highly dynamic, with discharge ranging from 9.5 to 123 m^3 s^{-1}, water velocity from 0.2 to 1.3 m s^{-1}, and water depth from 2 to 3 m. The River Rur has two smaller side rivers, the Inde and the Wurm, which also originate in the Ardennes near the Belgian border (Fig. 1). The River Swalm (catchment surface area of 277 km^2) originates near the city of Wegberg (Germany) (at 85 m a.s.l.), flows through Germany (31 km) and The Netherlands (12.2 km), where it discharges into the River Meuse (at 14 m a.s.l.). The channel width varies between 3 and 10 m, discharge ranges from 0.5 to 15 m^3 s^{-1}, water velocity from 0.1 to 1.0 m s^{-1}, and channel depth from 0.3 to 1.0 m.

Field survey

During 7–28 July 2003, the entire longitudinal courses of the Swalm and Rur Rivers (and their tributary streams) in Germany and The Netherlands (Fig. 1), were surveyed by boat (in wider and deeper stretches) or by wading through or walking along the river (in smaller and shallower stretches). The water was clear and visibility high (the bottom of the rivers was usually visible, except in certain stretches of the Rur river, deeper than 2.5 m), allowing the monitoring of submerged plants by visual census. Geographic locations and approximate number of individuals (as estimated on a log scale: 1, one individual; 2, two to 10 individuals; 3, 11–100, etc.) of *S. emersum* and *S. sagittifolia* populations were recorded on detailed geographic maps (1 : 10 000), which contained enough landmarks to pinpoint the exact locations of each population. During the field survey, ducks observed were also recorded.

Experimental design

Ripe seeds of *S. sagittifolia* and *S. emersum* were collected during autumn 2001 from natural populations in the Netherlands. Earlier tests showed that seeds of both species needed to be stratified (i.e. subjected to cold temperature while being imbibed in water) for an extended period to break seed dormancy (see also Muenscher, 1936). Therefore, the seeds were stored in glass jars filled with tap water, in a dark cold room at 5 ± 1 °C for 6 months, to mimic natural stratification conditions of Central-Northern European winters.

We used 10 mallard and 10 teal in our feeding experiments. Mallard had been captured in the wild
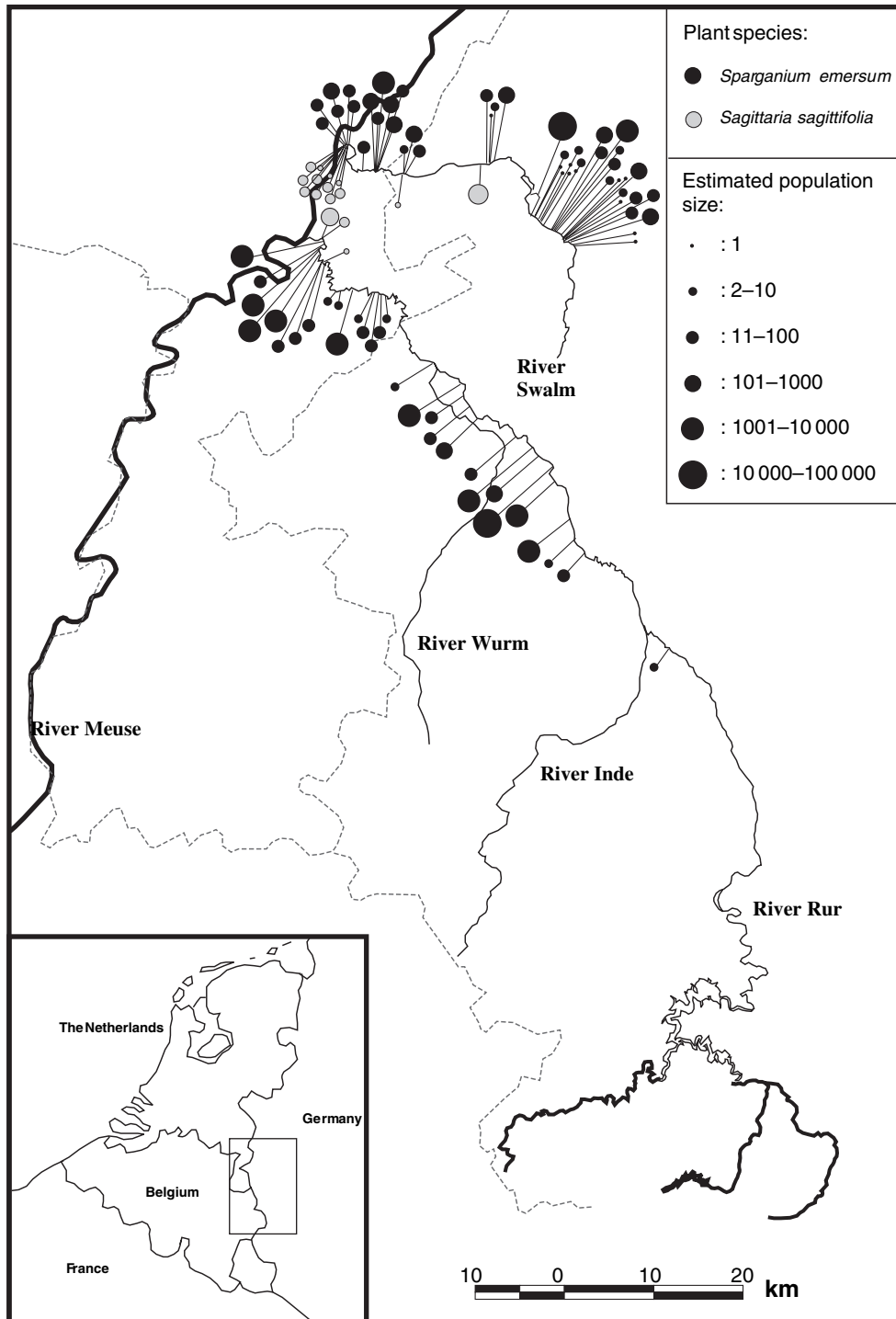
Fig. 1 The location of the study area in north-western Europe and the distribution of *S. emersum* (black dots) and *S. sagittifolia* (gray dots) in the Swalm and Rur rivers and their tributaries. The sizes of the dots are proportional to the number of individuals (upper right-hand panel). The dashed lines represent the country borders.

1 year before, while teal were born in captivity and obtained from Kooij & Sons Waterfowl Breeding Farm, The Netherlands. Prior to the experiments, all indivi- duals were housed in outdoor waterfowl facilities (Centre for Terrestrial Ecology, NIOO-KNAW at Heteren, The Netherlands) and kept on a stable diet

of commercial pellets (Anseres 3®; Kasper Faunafood, Waalwijk, The Netherlands) and mixed grains (Havens Voeders, Maashees, Cary, NC, U.S.A.). In the experiment, an even number of males and females of each duck species was used to detect potential differences in digestion and retention between genders. There were significant differences in animal weight between the duck species and genders, with mallard (mean ± SE: males 1.164 ± 0.04 kg, $n = 5$; females 1.003 ± 0.03 kg, $n = 5$) weighing approximately four times as much as teal (males 0.268 ± 0.01 kg, $n = 5$; females 0.258 ± 0.01 kg, $n = 5$).

At the beginning of the feeding experiment, each duck was force-fed 200 seeds (100 *S. emersum* seeds and 100 *S. sagittifolia* seeds). To ensure randomisation, groups of 10 seeds were haphazardly taken from the complete batch of seeds and randomly assigned to the individual ducks. To facilitate force-feeding, seeds were placed in soft pellets made from Anseres 3® food pellets soaked in water. The pellets were placed one by one on the posterior part of the tongue and pushed down the pharynx, subsequently allowing the ducks to swallow the pellet. Immediately after the feeding, each individual duck was transferred to a separate wooden cage ($0.6 \times 0.5 \times 0.5$ m) where it was kept for the duration of the experiment. Water and food were provided *ad libitum* throughout the experiments. Produced droppings fell through a maze bottom (square mesh size 13 mm) into plastic containers, which were emptied at 4-h intervals for a period of 60 h. Collected droppings were immediately rinsed with tap water and sieved using a 500 μm square mesh size sieve (diameter of 19 cm). Retrieved seeds were transferred to plastic containers (100 ml) filled with tap water and stored at 6 °C for the remaining duration of the experiment.

The batch of control seeds received a similar pre- and post-experimental treatment as the seeds used in the feeding experiment (i.e. placed in soft pellets soaked in water, sieved with tap water and stored at 5 °C for the duration of the feeding experiment) to exclude possible effects of pre- or post-feeding treatment on the seeds. Control seeds were divided further into two treatments: intact seeds (control) versus scarified seeds (scarified). Seed scarification was aimed at simulating the physical effects of gut passage, by removing the seed coat and abrading the endocarp. The treatment was applied to four random batches with 25 seeds each. Intact, non-

scarified seeds included four random batches with 100 seeds each.

Immediately after the feeding experiment, ingested, scarified and control seeds were set to germinate in a climate chamber with a photoperiod of 16L/8D, a daytime irradiance of 160–180 μmol photons s^{-1} m^{-2} and a day/night temperature cycle of 25/15 °C. Seeds were placed in transparent polystyrene microtiter-plates (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 60 days.

Statistical analysis

Differences in total seed retrieval (i.e. the proportion of ingested seeds recovered in the droppings) were tested by means of Generalised Linear Modelling using the GLMMIX module of SAS (1996; SAS Institute Inc, Cary, NC, U.S.A.). Differences in retention time were tested in a survival analysis by fitting a Cox proportional hazards regression model to the retrieval time (i.e. time between ingestion and retrieval, in hours) for each individual seed, using S-Plus 2000 (Mathsoft Engineering & Education Inc., Zoetermeer, The Netherlands). In both analyses plant species, duck species, duck gender and their second-order interactions were included as fixed factors, and the effect of different individuals was added to the model as a random (or fail try) effect.

The overall effects of plant species and seed treatment (i.e. intact, scarified and duck ingested) on total germination (i.e. proportion of seeds that germinated by the end of the germination run) were tested using Generalised Linear models (as above), followed by pairwise, *post hoc* tests comparing the different treatments within each plant species (with a $P < 0.008$ comparisonwise error rate, after Bonferroni correction). A separate analysis included retention time as a continuous independent variable plus duck species and duck gender as fixed factors, but only for total germination of *S. emersum* seeds (because of low retrieval, the analysis could not be performed for *S. sagittaria*). Heterogeneity of slopes was accounted for by selecting the best fit from a family of models that included all possible combinations (as both main factors and interactions) of the categorical factors and the continuous covariate, using the Akaike Informa-

tion Criterion. Differences in seed germination rates were tested by fitting a Cox proportional hazards regression model to the number of days between setting for germination and seedling emergence, for each individual seed that germinated (non-germinated seeds were excluded from the analysis to separate the effects of germination rate from those on total germination). For each plant species we fitted separate models, which included the same factors for total germination, described above.

Results

Field survey

The upper reach of the Rur (from its origin to the city of Julich, Germany) has a mountainous character, with a high gradient and high water velocity, limiting the presence of aquatic vegetation; thereafter, the gradient is less and plants of the Sparganieto–Sagittarietum association are found in patches of the river with low water velocity (see also Friedrich & Meyer-Holtzl, 2003). The upper reach and several middle parts of the Swalm River are characterised by the presence of dense riparian forests (Carr and Alnus–Betula carr forests) leading to shading of the river bed, and consequently to the absence of aquatic vegetation.

In both rivers, *S. emersum* displayed a wider longitudinal distribution compared with *S. sagittifolia* (Fig. 1). *S. emersum* typically occupied all suitable slow-flowing and shade-free habitat patches along the longitudinal axis in the Rivers Rur and Swalm, while *S. sagittifolia* was restricted to the downstream reaches. Both plant species were absent in the Worm and Inde. During the monitoring of plant populations along both rivers in July, over 230 and 170 mallards were observed along the Rivers Swalm and Rur, respectively. Teal were not observed because they are migratory species, which are absent from The Netherlands during the summer.

Feeding experiments

A significant difference was found in the total seed retrieval between the two plant species ($F_{1,3984} = 19.92$, $P < 0.0001$), with retrieval being more than tenfold higher for *S. emersum* (22.65 ± 20.8%; mean ± SD) than for *S. sagittifolia* (1.60 ± 2.4%). As the duck faeces contained many seed fragments, especially during the

first 8 h, the rest of the ingested seeds were probably digested in the ducks' digestive tracts. Duck species ($F_{1,3984} = 0.77$, $P = 0.3793$) and duck gender ($F_{1,3984} = 1.11$, $P = 0.2931$) had no significant effect on the total seed retrieval. The analysis did show significant interaction effects between plant and duck, plant and gender and, duck and gender; however, the low number of retrieved *S. sagittifolia* seeds (Fig. 2), precludes a reliable interpretation of these results.

Seed retention time differed significantly between the two plant species (Cox regression: $\chi^2 = 43.30$, d.f. = 1, $P < 0.0001$). All *S. sagittifolia* seeds were retrieved within 4–12 h after ingestion, whereas seeds of *S. emersum* were still retrieved 60 h after ingestion (Fig. 3), suggesting a potentially much larger range
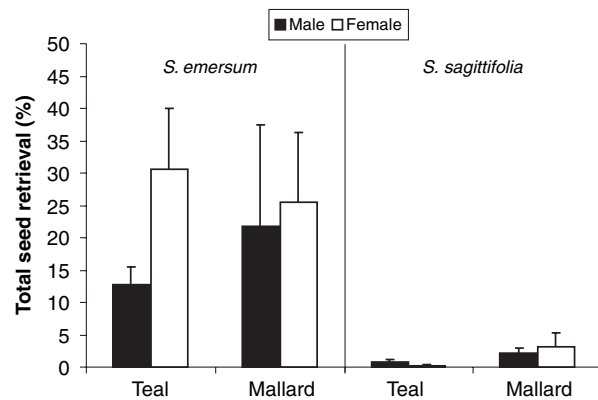

Fig. 2 Total seed retrieval (%) over 60 h, of *S. emersum* and *S. sagittifolia* seeds retrieved from mallard and teal (mean ± SE). Each duck was fed 100 seeds of each plant species. Black bars indicate retrieval from male ducks, white bars from female ducks ($n = 5$ ducks for each gender and species group).
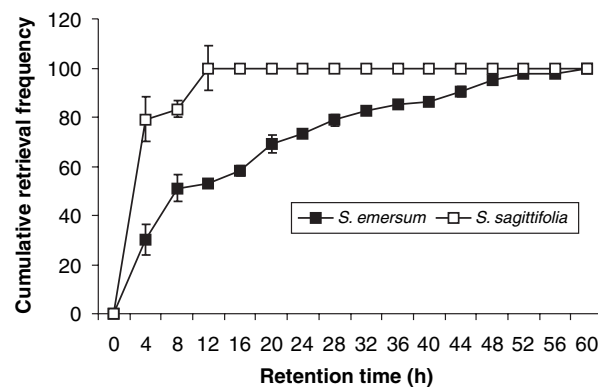

Fig. 3 Cumulative retrieval (%) of seeds over time for *S. emersum* and *S. sagittifolia* (mean ± SE; $n = 20$, 10 individuals for both mallard and teal). The experiment was terminated after 60 h.

distance of dispersal for *S. emersum*. The pattern of seed retrieval over time followed a leptokurtic curve for both plant species and did not differ significantly between duck species ($\chi^2 = 1.14$, d.f. = 1, $P = 0.290$) or gender ($\chi^2 = 0.49$, d.f. = 1, $P = 0.490$).

Total germination was significantly affected by plant species, being significantly higher for *S. emersum* compared with *S. sagittifolia* ($F_{1,17} = 103.16$, $P = <0.0001$). For *S. emersum*, control seeds showed lower total germination than duck-ingested and scarified seeds ($F_{1,925} = 8.41$ and 15.4, $P = 0.0038$ and 0.0001, respectively), which did not differ significantly from each other ($F_{1,925} = 4.94$, $P = 0.0265$; with a comparison-wise error rate of 0.008 after Bonferroni correction, for all three comparisons). For *S. sagittifolia*, control seeds showed higher total germination than scarified seeds ($F_{1,152} = 24.01$, $P = <0.0001$), whereas germination of duck-ingested seeds was intermediate between that of control and scarified seeds, and did not differ significantly from either ($P > 0.008$, Fig. 4a).

Retention time significantly affected the total germination of *S. emersum* seeds, with decreased germination at longer retention times ($F_{1,431} = 3.88$, $P = 0.0495$; Fig. 5). Total germination of retrieved seeds differed significantly between duck species, being higher for teal than for mallard ($F_{1,431} = 7.65$, $P = 0.0059$).

For *S. emersum*, control seeds displayed slower germination rate (i.e. number of days to germination) than duck-ingested and scarified seeds (Cox regression: $\chi^2 = 117.8$ and 86.7; d.f. = 1, $P < 0.0001$, respectively), which did not differ significantly between each other ($\chi^2 = 0.77$, d.f. = 1, $P = 0.38$; Fig. 4b). For *S. sagittifolia*, control seeds had faster germination rates than scarified seeds ($\chi^2 = 12.97$, d.f. = 1, $P = 0.0003$), whereas germination rate of duck-ingested seeds was intermediate between that of controls and scarified seeds, and did not differ significantly from any of these ($\chi^2 = 0.56$ and 7.54, d.f. = 1; $P = 0.450$ and 0.060, respectively). In a separate analysis on duck-ingested seeds, germination rate of *S. emersum* seeds was neither affected by duck species (Cox regression: $\chi^2 = 0.28$, d.f. = 1, $P = 0.600$) nor gender ($\chi^2 = 0.50$, d.f. = 1, $P = 0.480$).

Discussion

Differences between plant species

The effect of gut passage on ingested seeds is known to differ among plant species, largely owing to
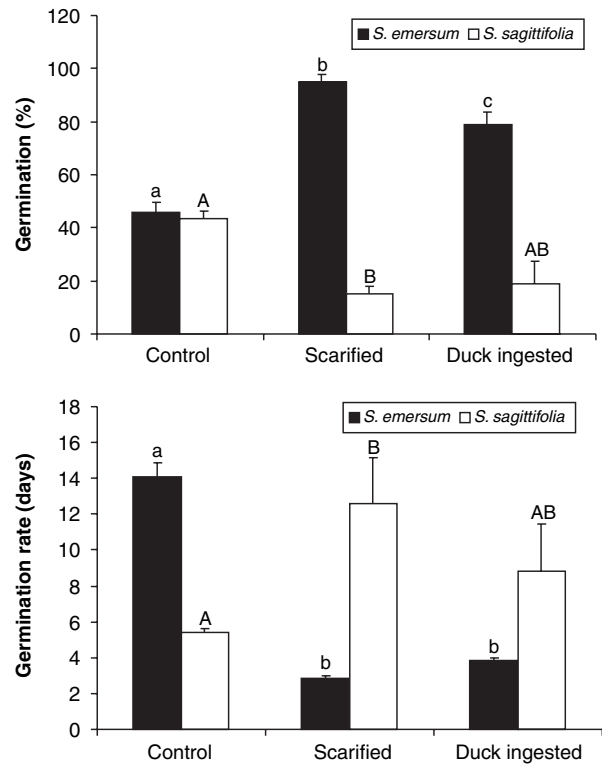

Fig. 4 Top: Proportion of germinated seeds (mean ± SE) and Bottom: day of germination (mean ± SE) of *S. emersum* (black squares) and *S. sagittifolia* (white squares) for the different seed treatments: control ($n = 400$, in four batches of 100 seeds), scarified ($n = 100$, in four batches of 25 seeds), and duck-ingested ($n = 453$ and 32 respectively, each in 20 batches with variable numbers of seeds). For each species, significant differences between treatments were indicated with letters (a, b, c, for *S. emersum*; and A, B for *S. sagittifolia*). Data points that do not share a common letter are significantly different from each other (see text for *P*-values).
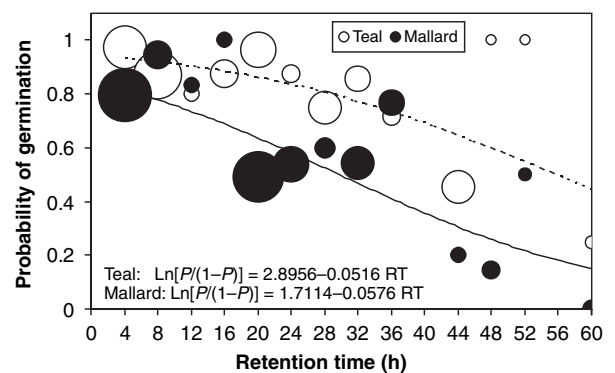

Fig. 5 Effect of retention time in the digestive tract of mallard (black dots) and teal (white dots) on the probability of germination of retrieved *S. emersum* seeds. Displayed equations were obtained from logistic regression after backward removal of non-significant factors. The sizes of the dots are proportional to the number of seeds, ranging from seven to 98.

differences in the structure of the seed coat (Proctor, 1968; Traveset, 1998; Traveset & Verdú, 2002). We hypothesised that seeds of *S. emersum* would show higher resistance to gut passage compared with seeds of *S. sagittifolia*, as they are enclosed in a hard scleridial endocarp and a tough spongy mesocarp. Seeds of *S. sagittifolia* have a soft membranous endocarp and fleshy mesocarp and are therefore more likely to be damaged or completely digested during gut passage (Traveset, 1998). The results indeed suggest that *S. emersum* has a higher potential for endozoochorous dispersal compared with *S. sagittifolia*. Firstly, a very small proportion of the ingested *S. sagittifolia* seeds was retrieved (1.60 ± 2.4%), more than fourteen times less than the proportion of *S. emersum* seeds that was retrieved (22.65 ± 20.80%). Secondly, all *S. sagittifolia* seeds were retrieved within the first 12 h after ingestion, whereas viable *S. emersum* seeds were still retrieved after a retention time of 60 h when the experiment was terminated, indicating a larger 'window of opportunity' for dispersal events to occur and a potential for much larger dispersal distances for *S. emersum*. Thirdly, retrieved *S. emersum* seeds displayed increased germination and higher germination rates, whereas retrieved *S. sagittifolia* seeds (which had lost the fleshy mecocarp and occasionally part of the membranous endocarp) showed decreased germinability and delayed germination rates, compared with non-ingested control seeds (Table 1).

The reduction in germination and germination rate of retrieved *S. sagittaria* seeds is most likely related to extensive grinding in the ducks' guts, partly bruising the seed embryo and affecting its capacity to germinate. Scarification of *S. sagittifolia* seeds resulted in a similar reduction of seed germination, suggesting that the mechanical treatment, rather then the chemical treatment, in the gut may be responsible for the observed reduction in seed germination. On the contrary, retrieved seeds of *S. emersum* displayed a significant increase in germination and germination rate, most likely related to the breaking of the seed-coat dormancy (Baskin & Baskin, 1998), which is necessary before germination can commence (Cook, 1962). Under natural conditions the seed coat of *S. emersum* can be broken after a period of freezing, or by natural decomposition. Passage through the digestive tract of waterfowl may similarly increase germination of seeds with a hard seed coat (Santamaria *et al.*, 2002). In fact, our results show that scarification (i.e. manual removal of the seed coat) increases the germination and germination rate significantly, suggesting that the mechanical treatment in the gizzard, that results in removal of seed coats, is responsible for the increased germination of seeds with a hard seed coat. Hence, our results (Table 1) suggest that *S. emersum* has a higher potential for endozoochorous dispersal by ducks and postdispersal establishment, while *S. sagittifolia* is less likely to undergo such a mode of dispersal.

Differences between duck species

Different duck species are likely to differ in their quality as endozoochorous seed dispersers, because of differences in their ecology, body size, gut morphology and digestive physiology (Charalambidou & Santamaria, 2002; Figuerola, Green & Santamaria, 2002; Green *et al.*, 2002). However, few studies have looked at differences in retrieval and subsequent germination success of seeds that have been ingested by different duck species.

In the present study, we found no significant difference in the total proportion of retrieved seeds between teal and mallard. The lack of observed interspecific differences is most likely because of the large

Table 1 Summary of the effect (mean ± SE) of seed ingestion by ducks on the retrieval (RT is the retention time) and germination of seeds of *S. emersum* and *S. sagittifolia*. The effect on germination was compared with intact control seeds.

Plant species	Seed structure (endocarp–mesocarp)	Retrieval		Germination	
		Max. RT (h)	Total retrieval (%)	Germination rate (days)	Total germination (%)
S. emersum	Hard scleridial endocarp and tough spongy mesocarp	60 h*	22.65 ± 20.8	Acceleration of 10 days	Increase of 33.3%
S. sagittifolia	Soft membranous endocarp and fleshy mesocarp	<12 h	1.60 ± 2.4	Delay of 3.5 days	Decrease of 24.4%

*Experiment was terminated at 60 h.

intra-specific variation among individuals (with the proportion of retrieved seeds ranging from 4 to 74%). Significant differences in seed retrieval over retention time between teal and mallard were not observed, despite the fourfold difference in body size between both species. Both species have similar feeding habits, both being opportunistic generalist feeders (Nummi, 1993) that display a seasonal diet shift from predominantly zoobenthivorous in spring and summer to predominantly granivorous in fall and winter. Both ducks can show changes in the size and morphology of their intestinal tract, in order to adapt to seasonal changes in food supply (Whyte & Bolen, 1985; Nummi, 1993). It has been suggested that such closely related *Anas* spp. have similar digestive physiologies (Miller, 1984), and that interspecific differences among these *Anas* spp. (such as differences in body size) may have little effect on retention time and digestion of seeds in their guts (Charalambidou, Santamaria & Langevoord, 2003).

Finally, we did find a significant difference between duck species in the total germination of retrieved *S. emersum* seeds. Total germination (%) of *S. emersum* seeds was slightly (although significantly) higher for seeds retrieved from teal compared with seeds retrieved from mallard. As germination of *S. emersum* seeds depends largely on the removal of the seed coat (see above), we suggest that the observed differences are because of a less efficient removal of the seed coat by mallard, compared with teal. Interestingly, this difference is, however, apparently strong enough to lead to a more efficient removal of the tough spongy mesocarp of *S. emersum* seeds in the intestinal tract, and therefore to a higher germination (%) of the retrieved seeds, whereas, it is not strong enough to be more damaging to the hard scleridial endocarp of *S. emersum* seeds, and hence does not lead to a difference in the total retrieval (%) of *S. emersum* seeds between duck species.

A mechanism for plant population persistence in rivers

The theory of what has become known as the 'drift paradox', was first formulated to describe the chronobiology of mobile stream organisms, such as invertebrates, amphibians and fish (Müller, 1974; Hersey *et al.*, 1993; Williams & Williams, 1993; Anholt, 1995). The theory states that population persistence in rivers depends on active upstream movement of individuals to compensate for the loss of individuals because of

downstream drift (Speirs & Gurney, 2001). However, many aquatic species, including aquatic macrophytes, lack a means of active upstream dispersal and for them the paradox of population persistence remained unresolved.

In this study, we investigated the potential for endozoochorous seed dispersal by waterfowl species. Although we did not conduct specific observations on the feeding behaviour of mallard and teal, we did observe that in October 2003 the ducks were often associated with plant populations of both species. As during autumn and winter they are predominantly granivorous feeders (McAtee, 1918; Metcalf, 1931; Martin & Uhler, 1939), ingestion of *S. emersum* and *S. sagittifolia* seeds by mallard and teal was likely to occur. Moreover, a preliminary study on the genetic population structure of *S. emersum* in the River Swalm, using microsatellites, provided some evidence for the occurrence of colonisation events to upstream areas (de Jong, 2004). We propose that plant population persistence in rivers is a dynamic process over a large time-scale, driven by two opposing forces: a steady downstream movement of populations because of unidirectional currents (Speirs & Gurney, 2001), counteracted by (possibly infrequent) upstream colonisation events because of animal-assisted dispersal. Particularly in rivers, animal-mediated seed dispersal may constitute an important component of dispersal of plants, through directional dispersal of seeds to empty niches in upstream areas. It has been suggested, that even infrequent upstream dispersal events would allow population persistence in river ecosystems, because depopulated upstream areas provide empty niches with little competition ensuring increased individual fitness to new colonists (Schupp, 1993; Anholt, 1995; Higgins, Nathan & Cain, 2003; Levine, 2003).

The present study is the first to implicate the potential importance of animal-mediated dispersal for plant population persistence in rivers. If so, differences between plant species in their ability to colonise upstream areas, may have consequences for their distribution in a river: species with a high potential of animal-mediated upstream dispersal and postdispersal establishment (i.e. *S. emersum*) may display a wider longitudinal distribution, compared with 'badly dispersed species' (i.e. *S. sagittifolia*), assuming that these areas provide suitable habitats for the plant species and animal vectors. The results from the field survey show that in the rivers Ruhr and Swalm (Fig. 1), *S.*

emersum indeed displays a higher upstream distribution compared with *S. sagittifolia* (Fig. 1). However, this single field survey provides only preliminary and circumstantial evidence for bird-mediated dispersal, and the mechanisms that determine plant population persistence in rivers require further research.

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