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Short communication

Intraspecific variation of seed floating ability in *Sparganium emersum* suggests a bimodal dispersal strategy

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ABSTRACT

Water-mediated spread of seeds (hydrochory) plays an important role in the dispersal of aquatic plants. In this study we investigate intraspecific variation in floating ability and germination capacity of *Sparganium emersum* seeds in relation to seed mass, within three natural populations along the Rur River (the Netherlands–Germany). Our results suggest that *S. emersum* produces two types of seeds: (i) short-floating seeds (SFS) that sink within 4 weeks (approximately 71% of all seeds), and (ii) long-floating seeds (LFS) that float at least for 6 months (approximately 28% of all seeds). Our study further shows that short-floating seeds display a significantly higher germination (%) (SFS = 89.9% vs LFS = 32.6%), a faster germination rate (SFS = 8.71 ± 3.3 vs LFS = 9.32 ± 3.1 days to germination) and a higher mean seed mass (SFS = 15.17 ± 4.5 vs LFS = 11.25 ± 3.8 mg), compared to long-floating seeds. It is argued that the production of these two types of seeds by *S. emersum* plants, each type with a different potential for water-mediated dispersal, represents a bimodal hydrochoric dispersal strategy.

1. Introduction

Dispersal plays a fundamental role in the life-history of plants, affecting their biology, ecology, (meta)population dynamics and genetics (Silvertown and Charlesworth, 2001). In river corridors, water-mediated spread (hydrochory) is considered to be the most important dispersal mechanism of aquatic plants (Sculthorpe, 1967). Seeds and vegetative plant parts (e.g. leaf and stem fragments, stolons, rhizomes, tubers, turions) of most aquatic and riparian plants display the ability to float for extended periods of time while remaining viable, thus potentially contributing to their downstream dispersal (Barrat-Segretain, 1996). In accordance, several studies have highlighted the importance of hydrochoric dispersal in structuring riparian plant communities along rivers (Nilsson et al., 1991; Jansson et al., 2005).

Seed buoyancy can vary considerably, both within and among plant species (Williamson et al., 1999; Van den Broek et al., 2005; Fumanal et al., 2007). Intraspecific variation in seed buoyancy may be related to either: (i) the production of distinctly different fruit morphologies by individual plants (seed heteromorphism, Venable, 1985), such as the dimorphic fruits of *Cakile edentula* (Payne and Maun, 1981) and *Spergularia marina* (Telenius and Torstensson, 1989); or (ii) the production of seeds with a continuous variation in fruit traits (cryptic seed heteromorphism, Venable, 1985), as in *Swartzia polyphylla* (Williamson et al., 1999) and *Ambrosia artemisiifolia* (Fumanal et al., 2007).

Unbranched burreed, *Sparganium emersum* Rehmann 1871 (*Sparganium simplex* Hudson 1778) (Sparganiaceae) is an aquatic, facultatively clonal, vascular macrophyte that is widely distributed throughout Eurasia and North America (Cook and Nicholls, 1986; Pollux et al., 2007a). It typically grows in a wide band at the margins of rivers and streams that are characterized by shallow, slow flowing waters. Its fruits (hereafter called seeds) are dispersed by water currents (Boedeltje et al., 2004), fish (Pollux et al., 2006, 2007b) and waterfowl (Pollux et al., 2005). In this study, we investigate the floating ability and germination capacity of *S. emersum* seeds within three populations along the Rur River (the Netherlands–Germany). Specifically, we ask: (i) What is the extent of variation in floating ability of *S. emersum* seeds among populations, among plants within populations and within single plants? (ii) Is there a difference in probability of germination and germination rate between short-floating and long-floating *S. emersum* seeds? (iii) Is floating ability, probability of germination or germination rate of *S. emersum* seeds related to their seed mass?

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2. Materials and methods

2.1. Experimental design

During 6–12 October 2003, ripe seeds of *S. emersum* were collected from three natural populations along the Rur River (Germany–the Netherlands): RUR ($50^\circ58'11.87''$N, $6^\circ16'41.60''$E), HIL ($51^\circ02'06.79''$N, $6^\circ13'51.02''$E) and ROE ($51^\circ10'54.72''$N, $5^\circ59'35.43''$E). In each population, 25 plants bearing mature seeds were randomly selected, and 100 seeds were randomly collected from each plant. In order to study the floating ability of *S. emersum* seeds, the seeds of each plant were placed in separate 500 mL glass beakers filled with 300 mL tap water and set to float for a period of 26 weeks. To mimic natural temperature stratification of Central–North European winters experienced by *S. emersum* seeds under natural conditions, the glass beakers were stored in a climate-controlled chamber at $5 \pm 1\,^\circ$C during the seed-buoyancy experiment. At regular times (at t = 1, 2, 3, 4, 6, 9, 12, 16, 20 and 26 weeks) the glass beakers were checked for seeds that had sunk. These were carefully taken out of the glass beakers using a pair of tweezers, placed in separate glass beakers filled with tap water and stored under the same conditions (at $5 \pm 1\,^\circ$C) for the remainder of the floating experiment. At the end of the 26-week seed floating-experiment, the wet mass of each seed was obtained by individually weighing the seeds on a SartoriusLP620P-microbalance after removing excess water using a paper cloth. The seeds were then transferred to transparent polystyrene microtiterplates (127 × 82 cm, 96 wells; Omnilabo International BV, Breda, the Netherlands) filled with tap water (one seed per well), and simultaneously set to germinate in a climate chamber with a 16 h photoperiod, a daytime irradiance of 200 μmol photons$\cdot$m^{-2} s^{-1} and a day/night temperature cycle of 25/18 °C. Germination, in our study defined as the emergence of the first foliage leaf, was checked daily for a period of 45 days.

2.2. Statistical analyses

Differences in the proportion of sunken seeds at different time intervals were tested by means of general linear modelling using the MIXED module for repeated measures in SAS 9.1.2, in which population (three levels) and floating time (11 levels: t = 0, 1, 2, 3, 4, 6, 9, 12, 16, 20 and 26 weeks) were included as fixed effects, plant individual as the subject effect and a compound symmetry model was used as the covariance structure (Littell et al., 1998). Differences among time intervals were assessed by separate sequential *post hoc* tests comparing the proportion of sunken seeds at time t with that of time $t+1$, with a P $(\alpha/10) < 0.005$ comparison-wise error rate after Bonferroni correction.

The probability of seed germination and germination rate (mean number of days to germination) were assessed by fitting generalized linear models to the data, using the GENMOD procedure in SAS 9.1.2. Models were fitted according to the Generalized Estimating Equations (GEE) method (Liang and Zeger, 1986) using the repeated statement with plant individual treated as the subject effect and an independent covariance structure (Stokes et al., 1995). The probability of seed germination (a dichotomous variable) was analysed using a binomial response distribution and a logit link function. Germination rate (a categorical variable based on random count data of number of days to germination) was analysed using a Poisson frequency distribution and a log link function (only considering seeds that had germinated by the end of the germination trial). Both types of analyses included two main effects, population and seed buoyancy (two levels: short-floating and long-floating seeds), and their interaction. Pair wise *post hoc* comparisons, using a Bonferroni adjusted comparison-wise error rate of $P(\alpha/3) < 0.0167$, were subsequently used to assess differences between short-floating seeds and long-floating seeds within each population separately.

Differences in seed mass were assessed by means of repeated measures ANOVA using the MIXED module (as above) with population, seed buoyancy and seed germination (two levels: germinated and non-germinated seeds at the end of the germination trials) as fixed effects and plant individual as the subject effect (Littell et al., 1998). Prior to the analyses data were either arcsine, square root transformed (proportion of floating seeds) or log(10) transformed (seed mass) to assure homoscedasticity and normality of residuals.

3. Results

The percentage of floating seeds decreased significantly over time (d.f. = 10, F = 615.99, $P < 0.0001$), revealing a remarkable dichotomy in floating behaviour which did not differ significantly among populations (d.f. = 2, F = 0.59; P = 0.5594; Fig. 1): seeds either sank within 4 weeks (hereafter referred to as the short-floating seeds (SFS); approximately 71% of all seeds), or remained floating until the end of the experiment, i.e. >26 weeks (hereafter referred to as the long-floating seeds (LFS); approximately 28%). Only few seeds (<1%) sank between 4 to 26 weeks. Notably, this dichotomy, marked by a 4-week boundary, was observed in each individual plant: i.e. each plant produced both short-floating and long-floating seeds. While the mean ratio of short-floating versus long-floating seeds was very similar among the populations (Fig. 1), it did vary among plants within populations: e.g. the percentage of long-floating seeds ranged from 0–64% in population RUR (mean ± S.D.: 27.68 ± 3.4%, N = 25 plants), from 0–71% in population HIL (mean ± S.D.: 28.88 ± 4.7%) and 0–64% in population ROE (mean ± S.D.: 30.60 ± 3.2%).

The germination (%) differed among the three populations (mean ± S.E.: 53.61 ± 9.6, 72.53 ± 6.6 and 59.86 ± 8.4% for RUR, HIL and ROE, respectively; d.f. = 2, χ^2 = 6.93, P = 0.0313), being significantly different between populations RUR and HIL (d.f. = 1, χ^2 = 6.85, P = 0.0089), but not between HIL and ROE (d.f. = 1, χ^2 = 0.61, P = 0.4366) or RUR and ROE (d.f. = 1, χ^2 = 3.12, P = 0.0773). Short-floating seeds displayed a higher germination (%) compared to long-floating seeds (d.f. = 1, χ^2 = 22.57, $P < 0.0001$), though a significant interaction effect (population × seed buoyancy: d.f. = 2, χ^2 = 11.76, P = 0.0028) suggested that this difference was not equally strong in each population. Indeed, *post hoc* tests, comparing the germination (%) of short-floating versus long-floating seeds within each population

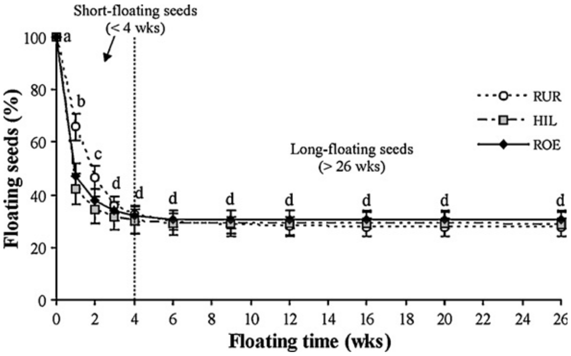

Fig. 1. Mean (±S.E.) proportion of floating seeds over a period of 26 weeks within three *Sparganium emersum* populations along the Rur River (based on N = 25 plants per population, 100 seeds per plant). Differences in mean (±S.E.) proportion of floating seeds between time points (at each time point the seeds of all populations pooled together) are indicated by letters, with time points that do not share a common letter being significantly different from each other (see text for P values).

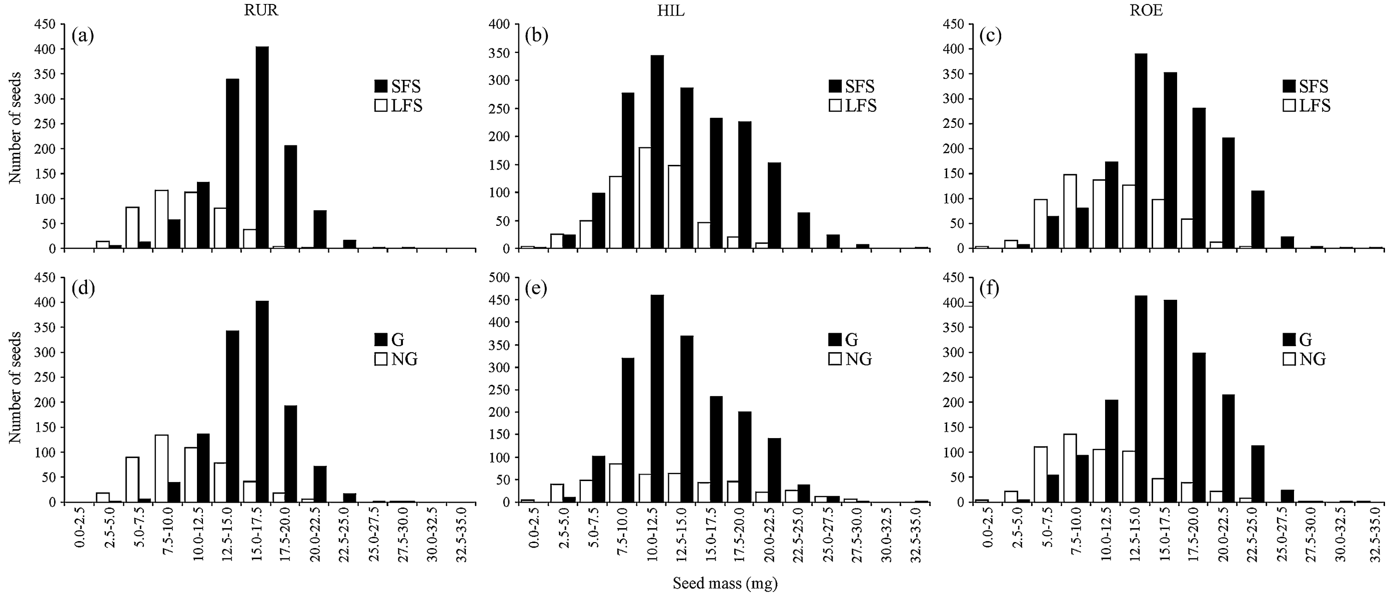

Fig. 2. Frequency distribution of seed masses (mg) within three *Sparganium emersum* populations along the Rur River (Germany–The Netherlands): (a–c) frequency distribution of seed mass of short-floating seeds (SFS; <4 weeks) and long-floating seeds (LFS; 4–26 weeks); (d–f) distribution of seed mass of seed that germinated (G) and those that did not germinate (NG) during the germination trials ($N = 25$ plants/population, 100 seeds/plant).

separately, showed this difference to be significant in populations RUR (mean ± S.E.: 89.14 ± 2.1% vs 16.39 ± 4.1%, respectively; d.f. = 1, $\chi^2 = 18.16$, $P < 0.0001$) and ROE (mean ± S.E.: 94.22 ± 1.2 vs 25.49 ± 7.0%; d.f. = 1, $\chi^2 = 17.44$, $P < 0.0001$) but not in population HIL (mean ± S.E.: 86.45 ± 2.9 vs 55.96 ± 8.2%; d.f. = 1, $\chi^2 = 5.09$, P = 0.0240; non-significant after Bonferroni correction).

The germination rate (mean number of days to germination) did not differ significantly between populations (RUR: 8.69 ± 2.4, HIL: 8.92 ± 4.2 and ROE: 8.74 ± 2.7 days; d.f. = 2, $\chi^2 = 0.71$, $P = 0.6996$). Overall, short-floating seeds had a higher germination rate (i.e. a lower mean number of days to germination) compared to long-floating seeds (d.f. = 1, $\chi^2 = 5.68$, $P = 0.0172$), though a significant interaction effect (population × seed buoyancy: d.f. = 2, $\chi^2 = 7.94$, $P = 0.0188$) suggested that this was not true in each population. In concurrence, *post hoc* tests subsequently showed that short-floating seeds displayed a significantly higher germination rate in populations RUR (mean ± S.D.: SFS = 8.57 ± 2.4 vs LFS = 10.06 ± 2.5; d.f. = 1, $\chi^2 = 22.43$, $P < 0.0001$) and ROE (SFS: 8.62 ± 2.6 vs LFS: 9.71 ± 3.1; d.f. = 1, $\chi^2 = 5.86$, $P < 0.0155$), but not in population HIL (SFS: 8.92 ± 4.4 vs LFS: 8.92 ± 3.2; d.f. = 1, $\chi^2 = 0.00$, $P < 0.9956$).

A significant difference in seed mass was found among populations (d.f. = 2, $F = 3.34$, $P = 0.0364$), with the mean (±S.D.) seed mass (mg) in population HIL (13.37 ± 4.9 mg) being significantly lower compared to population ROE (14.83 ± 4.9; $P = 0.0124$), but not compared to population RUR (14.03 ± 4.0; $P = 0.0791$). A significant difference in seed mass was also found between short-floating and long-floating seeds (d.f. = 1, $F = 34.69$, $P < 0.0001$), separate *post hoc* comparisons showing that in each population the short-floating seeds were significantly heavier than the long-floating seeds ($F_1 = 103.23$, $P < 0.0001$; $F_1 = 8.50$, $P = 0.0042$; $F_1 = 44.45$, $P < 0.0001$ within populations RUR, HIL and ROE, respectively; Fig. 2a–c). Significant differences in seed mass were furthermore observed between seeds that germinated and those that did not germinate (d.f. = 1, $F = 667.19$, $P < 0.0001$), within each population the seeds that germinated being significantly heavier than the seeds that did not germinate ($F_1 = 287.75$, $P < 0.0001$; $F_1 = 139.05$, $P < 0.0001$; $F_1 = 324.07$, $P < 0.0001$ within populations RUR, HIL and ROE, respectively; Fig. 2e–f).

4. Discussion

4.1. A bimodal dispersal strategy in S. emersum

The seed floating experiment revealed a strong dichotomy in floating behaviour of *S. emersum* seeds: seeds either sank within 4 weeks (approximately 71% of all seeds) or remained floating until the end of the experiment (approximately 28%), with virtually no seeds displaying an intermediate sinking behaviour (<1% of all seeds; Fig. 1). It may be argued that this observed dichotomy in buoyancy among seeds will have implications for their probability of dispersal: seeds of *S. emersum* reach full maturity in autumn (Sept-Oct), at which time they are released into the water. The majority of seeds, however, is trapped in the matrix of dense vegetation along the shore until the above-ground vegetation disappears due to winter decay, typically 6–8 weeks after seed release (B. Pollux, personal observation). Consequently, the majority of the short-floating seeds are likely to sink in their own population before the above ground biomass has disappeared. The long-floating seeds, on the other hand, will be dispersed by water currents to downstream locations as soon as the above ground vegetation has gone. Thus, the production of short-floating and long-floating seeds by single *S. emersum* plants may translate in different probabilities of dispersal: (i) short-floating seeds may be locally dispersed, ensuring recruitment within the population, while (ii) long-floating seeds may potentially be dispersed over long distances, allowing for colonization of new habitats and gene flow among populations. These findings are in accordance with the outcome of a recent study investigating the rate of gene flow and genetic diversity within and among nine *S. emersum* populations in the Niers River (the Netherlands–Germany). This study showed that approximately 65–80% of the individuals in a population resulted from of local recruitment while 20–35% of the individuals were due to dispersal among populations (Pollux, 2007). This, together with the observed dichotomy in floating behaviour of *S. emersum* seeds in this study, is strongly indicative of a bimodal dispersal strategy in *S. emersum*.

Seed buoyancy in *S. emersum* appears to be related to seed mass, with short-floating seeds having a significantly higher seed mass than long-floating seeds (SFS = 15.17 ± 4.5 and LFS = 11.25 ± 3.8 mg, respectively). In terrestrial plants that rely on wind-mediated seed dispersal, dispersal distance is often a direct function of seed mass and wind velocity, with lighter seeds being dispersed over greater distances than heavier ones (Greene and Johnson, 1993; Soons et al., 2004). However, in aquatic plants that rely on water-mediated dispersal, seed buoyancy, and hence presumably dispersal distance, is not necessarily directly related to seed mass (e.g. Ikeda and Itoh, 2001). Seeds consist of an embryo and endosperm (seed reserve) enclosed by a protective seed coat, and it is the morphological structure of the seed coat that generally conveys positive buoyancy to seeds: e.g. spongy or cork-like tissues that contain trapped air (air pockets), external structures that increase the surface-area-to-volume ratio (e.g. hairs or wings), and/or water-impermeable, waxy, cuticularized epidermi of the testa (Sculthorpe, 1967). Williamson et al. (1999) suggested that a discontinuous dimorphic trait such as seed buoyancy (floating vs non-floating seeds) may result from a continuous variation in other seed traits (i.e. cryptic seed heteromorphism, Venable, 1985) leading to continuous variation in specific gravity around a mean near 1 (<1 being non-buoyant; >1 being buoyant). In this study, the observed bimodal buoyancy of *S. emersum* may likewise be related to the production of seeds with a continuous variation in fruit traits, such as embryo size/mass, amount of endosperm and/or total volume of internal air pockets (buoyancy of *S. emersum* seeds is caused by the presence of numerous air-filled cavities in the exocarp; Cook and Nicholls, 1986; Barrat-Segretain, 1996). This, in turn, may have translated into the observed differences in seed mass between short-floating and long-floating *S. emersum* seeds (e.g. Williamson et al., 1999). However, further in-depth research is required to examine how micro-morphological variations in seed (coat) structure may lead to intraspecific variation in specific gravity (and hence buoyancy) of seeds, not only in *S. emersum* (this study) but also in other aquatic plant species (e.g. Williamson et al., 1999; Ikeda and Itoh, 2001; Fumanal et al., 2007).

4.2. Germination

Although *S. emersum* seeds are produced in autumn, they remain dormant until spring next year. This strategy has two advantages: (i) it ensures that seeds do not germinate until spring when conditions (water temperature, photoperiod) become optimal for growth and survival of young seedlings and (ii) it allows for a dispersal phase during which the dormant seeds can be dispersed (Boedeltje et al., 2004).

Our study shows that short-floating *S. emersum* seeds have a significantly higher germination (%) (SFS = 89.9% and LFS = 32.6%, respectively) and a (slightly) faster germination rate (SFS = 8.71 ± 3.3 and LFS = 9.32 ± 3.1 days to germination, respectively) compared to long-floating seeds. The observed differences in germination (%) are consistent with findings by Keogh and Bannister (1993) and Fumanal et al. (2007) who reported similar differences between short- and long-floating seeds in *Discaria* sp. (100 vs 33%) and *A. artemisiifolia* (80.2 vs 55.2%), respectively. Such differences in germination (%) and germination rate between short-floating and long-floating seeds may be due to two different reasons: first, long-floating seeds may display a higher degree of dormancy compared to short-floating seeds. Indeed, most studies suggest that heavy, non-dispersed seeds are generally less dormant than lighter, dispersed seeds (Rees, 1996; Olivieri, 2001). In our study we found that short-floating (and presumably non-dispersed) *S. emersum* seeds have both a higher seed mass and a (slightly) faster germination rate, than long-floating (and potentially long-distance dispersed) seeds. Hence, it is possible that the lighter, long-floating *S. emersum* seeds display a higher degree of dormancy (Rees, 1996; Olivieri, 2001). Second, long-floating seeds may have a lower viability compared to short-floating seeds. Several studies have demonstrated positive relationships between seed mass and the probability of germination, both within and between plant species (Milberg et al., 2000; Baloch et al., 2001; Daws et al., 2004). Decreased viability of smaller seeds may be related to a variety of factors, such as increased light dependence (Milberg et al., 2000), decreased dessication tolerance (Daws et al., 2004) or the use of different energy storage materials (since seed dispersal of terrestrial wind-dispersed plants is more effective when seed mass is low, it has been suggested that smaller seeds may be packed with lighter energy sources such as fat and consequently be viable for a shorter period of time than larger seeds; Rees, 1996; Olivieri, 2001). Unfortunately, as we did not assess viability of non-germinated seeds at the end of the germination trials (e.g. with tetrazolium tests), we are unable to state whether the observed differences in germination percentage between short- and long-floating seeds are due to differences in dormancy (hypothesis 1) or viability (hypothesis 2).

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