Seed size regulates plant dispersal distances in flowing water

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Abstract

1. Dispersal is an essential component of plant life, especially under the current threats of anthropogenic habitat fragmentation and climate change. For many wetland species, water is a key dispersal vector, as it can presumably disperse seeds long distances and towards suitable sites for establishment. Seed dispersal distance is affected by stream characteristics and seed traits. Yet, the effect of relevant seed traits, such as size, remains largely unknown.

2. Here, we report on an experimental field study examining the effect of seed size on dispersal distance in lowland streams. We released cork seed mimics of different sizes in four Dutch lowland streams in restored and channelized sections. After 24 hr, we recorded their entrapment location, entrapment mechanism, and the vegetation type in which they were caught.

3. Large seeds generally dispersed over longer distances than smaller seeds. This effect of seed size is likely caused by the different entrapment mechanisms—net trapping, surface tension, and wake trapping—which were highly correlated with seed size. Especially net trapping was responsible for the capture of a large proportion of small seed mimics in vegetation such as aquatic and riparian grasses, starwort, and reed. Due to the prevalent occurrence of these vegetation types in lowland streams, particularly during summer, smaller seeds are more likely to become entrapped and, hence, disperse less far. Our analysis on existing seed data reveals that water-dispersed riparian plants have relatively large seeds and are thereby evolutionarily adapted to long-distance dispersal. Furthermore, our results indicate that median dispersal distances are 0.02–1.8 km (99-percentile <8.5 km) in lowland streams in summer. In winter, less vegetation is present in and surrounding the streams, which leads to median dispersal distances of 0.12–14.2 km (99-percentile <65 km).

4. Synthesis. This study demonstrates that (a) large seeds generally disperse further than smaller seeds in lowland streams and (b) distances depend strongly on stream vegetation. This information should inform future restoration, for instance, by planning efforts to coincide with times or conditions of open water which are more favourable for the dispersal of target plant species—especially those with small seeds (<10 mm).
1 | INTRODUCTION

Dispersal is of key importance for the persistence of species, especially in response to anthropogenic changes, such as habitat fragmentation and climate change (Nathan et al., 2008). Plant species growing in riparian habitats (i.e., bordering streams and rivers) are often dispersed by surface water flows and many of these species produce seeds with adaptations for water dispersal (hydrochory; Boedeltje, Bakker, Bekker, Van Groenendaal, & Soesbergen, 2003; Nilsson, Brown, Jansson, & Merritt, 2010; Soons et al., 2017). Stream water has the potential to transport seeds over long distances and to deposit seeds at sites with suitable hydrological conditions for plant species recruitment and survival (directed dispersal; Fraaije, ter Braak, Verduyn, Verhoeven, & Soons, 2015; Soons et al., 2017). Although other dispersal mechanisms are required to disperse seeds upstream and between catchments (Wubs et al., 2016), dispersal by water is often considered the main dispersal vector for many riparian species.

Water dispersal potential of plant species is greatly altered due to global human modifications in the hydrodynamics and flooding regimes of streams and rivers (Nilsson et al., 2010), leading to the critical decline of many water-dispersed species across heavily modified landscapes (Ozinga et al., 2009). To help reduce species loss and inform restoration efforts, it is becoming increasingly relevant to understand the mechanisms that determine water dispersal of riparian plant species. Over the last decade, numerous projects have been initiated to restore stream sections across Western Europe, where most streams have been channelized during the previous century to better control water flows (Verdonschot & Nijboer, 2002). Changes in stream morphology have been shown to have significant impacts on how far seeds can travel, and where they will land (Engstrom, Nilsson, & Jansson, 2009); channelizing waterways therefore has had a number of negative effects on associated plant communities (Verdonschot & Nijboer, 2002). In an attempt to reverse this damage, stream restoration projects have become increasingly prevalent. Colonization of restored stream sites and maintenance of gene flow between populations is of vital importance for the survival of riparian plant communities, yet seed dispersal distances have not been taken into account in current and past stream restoration projects (Flavio, Ferreira, Formigo, & Svendsen, 2017; Heino et al., 2017). If we are able to estimate dispersal distances of water-dispersed plant species, we can use this knowledge to generate more accurate predictions of a species’ potential to colonize new areas, its gene flow, and the success rate of restoration measures (Brederveld, Jaehnig, Lorenz, Brunzel, & Soons, 2011).

The dispersal distance of water-dispersed seeds is influenced by the interaction between extrinsic (physical characteristics and hydrology of the river or stream) and intrinsic factors (traits of the propagules themselves; Chambert & James, 2009; Nilsson et al., 2010). While morphological adaptations to dispersal by water, such as seed size, seed shape, or structures to increase buoyancy, may aid dispersal of plants that grow in frequently inundated areas, their effect on water dispersal has rarely been studied in situ (Andersson, Nilsson, & Johansson, 2000; Hampe, 2004; Kaproth & McGraw, 2008; Merritt & Wohl, 2002; Säumel & Kowarik, 2010, 2013). Seed size is an intrinsic factor that may affect seed dispersal distance distributions and varies widely between species, within species, and even within individuals (Delefosse, Povidisa, Poncet, Kristensen, & Olesen, 2016; Garcia-Nogales, Linares, Laureano, Seco, & Merino, 2016; Piwowarczyk, Halamski, & Durska, 2014; Qi et al., 2015). Few studies have focused on the effect of seed size on hydrochorous dispersal distance, and these have yielded somewhat contradictory outcomes (Chambert & James, 2009; Säumel & Kowarik, 2010, 2013; Sousa, Kennedy, Mitchell, & Ordonez, 2007). Sousa et al. (2007) observed that small seeds were dispersed further than larger seeds in three mangrove species. In contrast, Säumel and Kowarik (2010, 2013) found an opposite relation for the seed dispersal of three invasive tree species in river systems. Chambert and James (2009) concluded that no consistent correlation can be found between seed characteristics such as seed size and dispersal distances of buoyant seeds.

In order to gain a better understanding of dispersal distances of water-dispersed seeds, we investigated the effect of seed size on water dispersal potential. Specifically, we explored (i) how far seeds of different sizes disperse in lowland streams, (ii) how vegetation mediates seed dispersal distances and deposition sites, (iii) which mechanisms are responsible for seed deposition along the stream banks, and (iv) how seed size varies in natural populations of plant species.

On the one hand, we expected smaller seeds to move along with the water flow through small gaps in the vegetation more easily than larger seeds (which become entrapped by way of net trapping), resulting in smaller seeds being dispersed over longer distances. On the other hand, small seeds should adhere more easily to branches and leaves by means of surface tension, resulting in further dispersal of large seeds. In order to obtain results for a relevant and representative range of systems, we addressed these questions in both channelized and restored sites. With respect to the role of vegetation, we expected that more finely branched plants present in the water column entrap more seeds than those on the banks or than sparsely branched plants, thereby limiting seed dispersal distances. To test these hypotheses, we released floating seed mimics of different sizes in channelized and seminatural (restored) streams and recorded their speed, entrapment locations, and entrapment mechanisms. We
used these data to calculate how seed size affects seed dispersal kernels under channelized and restored conditions. Furthermore, we performed a meta-analysis on existing seed size data. In highly dynamic environments such as riparian systems, a high dispersal capacity is essential to maintain population persistence in the landscape (Cheptou, Hargreaves, Bonte, & Jacquemyn, 2017). If large seeds disperse further than smaller seeds via water, we expected plant species that inhabit stream banks (i.e., helophytes) to have larger seeds than species that are less likely to be dispersed over the water surface (i.e., submerged species and upland species; Soons et al., 2017). However, if small seeds disperse further than larger seeds, we would expect no substantial difference in seed size between helophytes and upland species, as small seeds in general are also dispersed further by wind than larger seeds.

2 | MATERIALS AND METHODS

2.1 | Study system

The field experiments were performed in two reaches per stream (one channelized and one restored) in four lowland streams in the Netherlands (the Hagmolenbeek (52°21’N, 6°73’E), the Hegebeek (52°16’N, 6°87’E), the Rolderdiep (53°03’N, 6°66’E), and the Tungelroyse Beek (51°22’N, 5°65’E)), which we selected for their representativeness in stream characteristics, such as stream size, surrounding vegetation, and for ease of access and the existence of nearby channelized and restored stream sections within each stream. Restored stream sections had been renovated to their pre-channelized state, with a meandering waterway and gradually sloping, broader, and shallower profile with a larger riparian zone instead of the steep slopes and straight passages that are characteristic of channelized streams. The selected streams were lowland, sandy substrate streams ranging between 1.5 and 8.0 m in width. Because one channelized section was deeper than 1.5 m, we were unable to wade through and use it as an experimental site, resulting in a total of seven experimental stream sections. More details regarding the stream sections used in this experiment can be found in Table S1.

2.2 | Effect of seed size on dispersal distances

To quantify how far seeds of different sizes disperse in lowland streams, we released cork seed mimics into the seven stream locations described above and in Table S1. Seed mimics were made of cork discs in five different sizes (2.5, 5, 10, 15, and 20 mm diameter), each with a thickness of 2 mm. The largest mimic size (20 mm) was selected as this is the smallest possible size to hold a PET tag, which informed us on dispersal speeds. The minimum mimic size was determined by visibility; the 2.5-mm mimics were retrieved less often than the 5-, 10-, 15-, and 20-mm seed mimics and therefore no smaller sizes were included. Actual seed sizes of riparian vegetation fall within (and below) the selected range (see Section ). In summer 2015 and winter 2015/2016, we used the four biggest sizes in our release experiments; in spring 2016, we added the 2.5-mm seed mimics to investigate the effect of even smaller seed sizes. We tested the seed mimics for buoyancy and observed that the cork would stay afloat over >48 hr, even while perturbed. To aid retrieval of the mimics, we spray painted them in a variety of colours using biodegradable paint. We released 250 mimics of each size, in randomized batches of 50 to avoid interference, at the start of a section and retrieved these 24 hr after release. The 20-mm discs carried PET tags, which could be read at five equidistant points along the stream section by PET tag readers (consisting of a single coil antenna with tuning adapter and IP67 red connector, a decoder box holding a LID650-Multi decoder, antenna driver, clock-calendar, and internal memory, and a 12V-33Ah sealed lead battery; Dorset IDentification, Aalten, the Netherlands) to log their velocities. During seed mimic retrieval, we recorded the distance from the starting location (with an accuracy of 2.5 m) and their entrapment situation (see below). Mimics that travelled further than a maximum dispersal distance of 100–300 m (based on earlier mimic release trials per stream) were retrieved by a net that was placed over the water, which we constructed to be able to collect all mimics within a day.

2.3 | Relation between seed size and dispersal distance per field experiment

For each stream and each seed mimic size, we transformed the distance data into an inverse cumulative frequency distribution, showing the frequency of events of a seed dispersing further than dispersal distance X (Fx ≥ X; see Figure 1). Assuming that stream characteristics are similar throughout a stream section, this inverse cumulative frequency distribution corresponds to exponential decay (Johansson & Nilsson, 1993; Nilsson et al., 2010; Tackenberg, Poschlod, & Bonn, 2003):

\[
F(x) = \lambda^x,
\]

(1)

where \( 0 < \lambda < 1 \) depends on stream characteristics and seed size. Because \( \lambda \) cannot be larger than 1 (e.g., the frequency would increase rather than decrease with distance) or smaller than 0, we assume a sigmoidal correlation between seed size and \( \lambda \):

\[
\lambda = 1 - (1 + e^{a+bS})^{-1},
\]

(2)

where S is the seed size in mm diameter and a and b define the slope of the sigmoid curve (b) and the point where \( \lambda = 0.5 \) (equal to \( a/b \)). By taking Equations 1 and 2 together, we can derive a linear relationship between the observed dispersal distances and seed size:

\[
\ln[-\frac{x}{1-x}] = a + bS
\]

(3)

2.4 | Potential seed dispersal distances

Using the parameters a and b that we estimated from the field data (Table S2), we calculated the 99 percentile dispersal distance \( X_{99} \):

\[
X_{99} = \ln(0.01) \cdot \ln(\lambda)^{-1}.
\]

(4)
2.5 | The role of vegetation in seed deposition

To establish how vegetation mediates seed dispersal distances and deposition sites, we examined the effect of different types of vegetation on seed entrapment. We allocated the standing vegetation in and bordering the streams to 12 vegetation types (Table S3). During seed mimic retrieval, we recorded the vegetation type that entrapped the seed mimic. A general vegetation survey was performed every 5 m in spring and every 10 m in summer and winter along each experimental section to record coverage by each vegetation type, in order to examine which vegetation types trap more seeds than expected by their abundance.

2.6 | Seed entrapment mechanisms

To establish which mechanisms are responsible for seed deposition along the stream banks, in spring, we also recorded the entrapment mechanisms of each seed: net trapping, surface tension, or wake trapping. We expected that seeds of different sizes are entrapped by different mechanisms, thereby influencing seed dispersal distances. In net trapping, parts of the vegetation (living or dead) within a stream form a net-like structure that functions as a barrier to seed movement downstream (Defina & Peruzzo, 2010). Surface tension can trap seeds by means of the capillary effect known as the “Cheerios effect” (Vella & Mahadevan, 2005), where the seeds are drawn to and thereafter attach to a structure, such as a stem. Finally, wake trapping occurs when seeds get trapped behind an obstacle in the stream flow and remain within this area throughout the experiment (Peruzzo, Defina, & Nepf, 2012; White & Nepf, 2003). Defina and Peruzzo (2010) demonstrated that net trapping is the most common seed entrapment mechanism; yet it is unknown how seed size and vegetation characteristics affect the occurrences of the different entrapment mechanisms. Initially, we intended to also include inertial impaction, where seeds are forced onto the stream banks by their inertia and are entrapped behind obstructions such as plant stems (Palmer, Nepf, & Pettersson, 2004). However, as we recorded only very few seeds entrapped by means of inertial impaction, we could not statistically test any relations with entrapment by inertial impaction and excluded these data from our analyses.

2.7 | Seed size variation in natural populations

We investigated possible adaptations of seed size to facilitate hydrochory by relating the seed size and seed volume (l·w·h) as recorded in the LEDA traitbase (Kleyer et al., 2008) to the Raunkiær life-form of plant species. We compared seed sizes between all hemicryptophytes, helophytes, and hydrophytes of which seed size data and Raunkiær life-form is available in the LEDA traitbase. Plant species that inhabit stream banks (helophytes) are most likely to have seeds dispersed by floating on the water surface, whereas more aquatic species (hydrophytes) are most likely to be dispersed as bed load, and more terrestrial plant species (hemicryptophytes) will be dispersed more frequently by wind (Soons et al., 2017). When the field experiment shows a positive correlation between seed size and dispersal distance, we would expect that helophytes have larger seeds than hydrophytes and hemicryptophytes.

2.8 | Statistical analyses

To investigate the relation between seed size and entrapment by different vegetation types, we used a linear mixed-effects model (lmer from the R-package lme4, using field site as a random factor) on the proportion of seed mimics of each size that was caught by different vegetation types. We examined the relation between seed size and three entrapment mechanisms—net trapping, surface tension,
TABLE 1 General overview of the dominant vegetation and main entrapment vegetation in each experiment. The last column shows the relation between entrapment probability and seed size; asterisks indicate the significance level of the relation between seed size and dispersal distance (*p < 0.05, **p < 0.01, ***p < 0.001; statistical details in Table S2)

| Stream section      | Dominant vegetation | Main entrapment vegetation | More large/small seeds entrapped? |
|---------------------|---------------------|-----------------------------|-----------------------------------|
| Hagmolenbeek        | Channelized         | Summer                      | Water lily                        |
| Hegebeek            | Channelized         | Summer                      | Aquatic grasses                   |
| Tungelroyse Beek    | Channelized         | Summer                      | Reed                              |
| Hagmolenbeek        | Restored            | Summer                      | Riparian grasses                  |
| Hegebeek            | Restored            | Summer                      | Dead vegetation                   |
| Tungelroyse Beek    | Restored            | Summer                      | Reed                              |
| Rolderdiep          | Restored            | Summer                      | Starwort                          |
| Hagmolenbeek        | Channelized         | Winter                      | Reed                              |
| Hegebeek            | Channelized         | Winter                      | Aquatic grasses                   |
| Tungelroyse Beek    | Channelized         | Winter                      | Reed                              |
| Hagmolenbeek        | Restored            | Winter                      | Riparian grasses                  |
| Hegebeek            | Restored            | Winter                      | Bare sediment                     |
| Tungelroyse Beek    | Restored            | Winter                      | Reed                              |
| Hagmolenbeek        | Channelized         | Spring                      | Reed                              |
| Hegebeek            | Channelized         | Spring                      | Bare sediment                     |
| Tungelroyse Beek    | Channelized         | Spring                      | Reed                              |
| Hagmolenbeek        | Restored            | Spring                      | Riparian grasses                  |
| Hegebeek            | Restored            | Spring                      | Roots                             |
| Tungelroyse Beek    | Restored            | Spring                      | Reed                              |

and wake trapping—using a linear mixed-effects model (with field site as a random factor). To examine the relation between seed size and seed dispersal distances, we used Equation 3 in a simple linear regression model. To test whether helophytes have larger seeds than hydrophytes and hemicryptophytes, we used an ANOVA. We used R (R Core Team, 2014) to analyse our experimental data.

3 | RESULTS

Out of the 19 field experiments, 10 showed a positive relation between seed size and dispersal distance (Figure 1), 1 a negative relation, and 6 field experiments showed no relation as seeds were either entrapped by large blockages or were not entrapped at all (Table 1; Figure S4). For all significant events (i.e., a significant relation between seed size and dispersal distance), we identified how the stream vegetation affected the relation between seed size and dispersal distance in the Supplementary Results (Data S5).

3.1 | Potential seed dispersal distances

Dispersal distances varied greatly across seasons (Figure 2). Seeds dispersed further in winter and spring than in summer (Wilcoxon paired rank sum test, p < 0.001 for summer–winter and summer–spring, p = 0.509 for spring–winter; Figure 2). This difference in dispersal distances was associated with variation in the percentage of open water in the stream (i.e., the surface of the stream not covered by vegetation). In summer, the streams were mostly covered by vegetation, whereas streams were more open in winter and spring. The difference in dispersal distance between the different stream sections (Table S6) can be largely accounted for by variation in the abundance of open water and of reed and riparian grass (Figure 3), which entrap relatively few seeds (see next section). Overall, seeds dispersed over short distances in summer, with median dispersal
distances ranging from 0.02 to 1.8 km (average across all stream sections: 0.2 km) and 99-percentile dispersal distances ranging from 0.1 to 8.4 km (average 1.4 km). Seeds are estimated to disperse over much longer distances in winter, with median dispersal distances ranging from 0.1 to 14.2 km (average across all stream sections: 3.0 km) and 99-percentile dispersal distances ranging from 0.6 to 65.5 km (average 13.8 km; Table S6).

3.2 | The role of vegetation in seed entrapment

Across all streams and seasons, water lilies, starwort, and aquatic grasses were the most common vegetation types in the streams, while reed, riparian grasses, and bare sediment were the most abundant types along the stream banks (Table 2). In-stream entrapment occurred most by floating debris, starwort, and aquatic grasses, while along the bank seed mimics mainly became entrapped in reed and riparian grasses (Table 2). When we consider the entrapment by vegetation types in relation to their occurrence, it becomes clear that the floating vegetation types, aquatic grasses, floating debris, and starwort, entrap significantly more seeds than expected ($p < 0.003$; Table 2), while the shoreline vegetation types, bare sediment, dead vegetation, reed, riparian forbs, riparian grasses, and tree branches, captured significantly fewer seeds than expected from their occurrence ($p < 0.001$; Table 2). No significant difference between the observed and expected number of entrapped seeds was found for common rush and roots along the shoreline and sturdy aquatic vegetation and water lilies in the stream.

3.3 | Effect of seed size on entrapment per vegetation type

Across all streams, seasons, and vegetation types, entrapment chance was most often negatively correlated with seed mimic size (Table 3a). The in-stream vegetation types, aquatic grasses, floating debris and starwort, and the along-stream vegetation types, common rush, dead vegetation, reed, and riparian grasses, all captured more small than large seeds (Table 3a). Riparian forbs and water lilies were the only vegetation types that entrapped more large seeds than smaller seeds. In the case of water lilies this relation was complex, as entrapment by water lily related positively with seed size in the

![FIGURE 3](https://via.placeholder.com/150)

**FIGURE 3** Seed dispersal distance, depicted here as the estimated 99 percentile dispersal distance of 10 mm seed mimics, is significantly correlated with (a) reed abundance, (b) grass abundance, and (c) the fraction of stream that is without vegetation (i.e., open water; linear model: $r^2 = 0.535$, $df = 16$, $p = 0.001$)

### TABLE 2 Observed versus expected entrapment of seeds per vegetation type. Observed numbers of seeds are seeds recovered in the experiments. Expected numbers of seeds are calculated from the relative abundance of the vegetation type within the stream and on the stream banks, and the total number of seeds entrapped by vegetation in that stream section. After Bonferroni correction ($\alpha = 0.05/17 = 0.003$), in-stream aquatic grass, floating debris, and starwort, entrap more seeds than expected by their occurrence. Bare sediment, dead vegetation, reed, riparian forbs and grasses, and tree branches entrap fewer seeds than expected.

| Vegetation type         | Number of entrapped seeds | Observed | Expected | $p$-value |
|-------------------------|---------------------------|----------|----------|-----------|
| Aquatic grasses         |                           | 1,113    | 983      | $0.003^*$ |
| Floating debris         |                           | 2,483    | 351      | $< 0.001^{**}$ |
| Starwort                |                           | 1,318    | 984      | $< 0.001^{**}$ |
| Common rush             |                           | 107      | 127      | 0.212     |
| Roots                   |                           | 433      | 482      | 0.105     |
| Sturdy aquatic          |                           | 109      | 151      | 0.011     |
| Water lily              |                           | 992      | 1,082    | 0.04      |
| Bare sediment           |                           | 579      | 1,004    | $< 0.001^{**}$ |
| Dead vegetation         |                           | 537      | 805      | $< 0.001^{**}$ |
| Reed                    |                           | 1,010    | 1,602    | $< 0.001^{**}$ |
| Riparian forbs          |                           | 228      | 403      | $< 0.001^{**}$ |
| Riparian grasses        |                           | 946      | 1,170    | $< 0.001^{**}$ |
| Tree branch             |                           | 86       | 272      | $< 0.001^{**}$ |

*$p < 0.003$; **$p < 0.001$. 

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TABLE 3  (a) T-values of linear mixed-effects models on the effect of seed size on the entrapment probability by different vegetation types. Underlined and bold T-values represent significant effects ($p < 0.05$) of seed size on entrapment probability. (b) The number of seeds entrapped per vegetation type and per entrapment mechanism during the spring experiments.

| Vegetation Type         | (a) Summer | (a) Winter | (a) Spring | (b) Spring |
|-------------------------|------------|------------|------------|------------|
|                         | Restored T-value | Channelized T-value | Restored T-value | Channelized T-value | Restored T-value | Channelized T-value | Net trapping (# seeds) | Surface tension (# seeds) | Wake trapping (# seeds) | Total trapping (# seeds) |
| Aquatic grasses         | −5.09      | 1.24       | NA         | −3.41      | NA         | −1.52      | 5            | 6            | 0          | 11          |
| Floating debris         | −1.72      | −1.03      | 1.00       | −1.50      | −0.41      | −2.78      | 278          | 14           | 0           | 292         |
| Starwort                | −1.38      | −0.62      | NA         | −2.31      | NA         | −2.32      | 153          | 20           | 0           | 173         |
| Common rush             | −2.51      | NA         | −1.15      | 0.73       | 0.18       | −0.37      | 19           | 2            | 0           | 21          |
| Roots                   | NA         | NA         | −1.30      | −0.38      | −0.66      | −1.40      | 348          | 44           | 0           | 397         |
| Sturdy aquatic          | −0.77      | 1.73       | 0.43       | −1.46      | −0.22      | −0.99      | 54           | 11           | 0           | 65          |
| Water lily              | 2.53       | −2.31      | NA         | NA         | 10.62      | NA         | 17           | 0            | 18          | 35          |
| Bare sediment           | −1.00      | −1.33      | −1.82      | −0.52      | −0.74      | −0.50      | 0            | 0            | 0           | 357         |
| Dead vegetation         | −1.67      | −2.13      | −0.59      | 0.80       | −1.49      | −1.79      | 146          | 70           | 0           | 216         |
| Reed                    | −0.74      | −7.16      | −1.24      | −2.39      | 1.52       | −0.16      | 415          | 58           | 23          | 496         |
| Riparian forbs          | 1.06       | 3.17       | NA         | −0.98      | NA         | −0.69      | 0            | 5            | 0           | 5           |
| Riparian grasses        | −0.87      | −2.60      | −0.49      | 0.36       | −0.13      | −0.67      | 66           | 10           | 0           | 76          |
| Tree branch             | 0.68       | NA         | 0.38       | −1.35      | −0.36      | 0.10       | 5            | 7            | 0           | 12          |
| All vegetation types    | −3.45      | −3.30      | −0.26      | −3.00      | −0.57      | −3.32      | 1,505        | 247          | 41          | 2,156       |
restored sections in summer and the channelized sections in spring, but negatively in channelized sections in summer. Furthermore, the density of entrapped seeds was higher in more dense vegetation (Figure 4; $df = 1279, t = 8.972, p < 0.001$), with smaller seeds more likely to become entrapped in dense vegetation than larger seeds ($df = 1279, t = -7.057, p < 0.001$).

### 3.4 Effect of seed size on entrapment per mechanism

In spring, we also noted the entrapment mechanisms of the seeds. The vast majority of seeds (appr. 82%; Table 3b) were entrapped by means of net trapping. Indeed, net trapping was the most prevalent mechanism for entrapment by almost all vegetation types (common rush, dead vegetation, floating debris, reed, riparian grasses, roots, starwort, sturdy aquatic vegetation, and water lily). Approximately 15% of the seeds were entrapped by surface tension, which was not a dominant entrapment mechanism for any vegetation type. Only few seeds were entrapped by wake trapping by water lilies and reed. For water lily, wake trapping was one of the two most occurring mechanisms (besides net trapping). Net trapping and surface tension entrapped more small seeds than larger seeds ($t = -2.663$, $df = 24$, $p = 0.007$ for net trapping; $t = -3.003$, $df = 24$, $p = 0.003$ for surface tension; Figure 5), while wake trapping showed the opposite
relation between seed size and entrapment chance ($t = 2.131, df = 16, p = 0.024$).

### 3.5 | Seed size variation in natural populations

Our analysis of seed trait data from the LEDA traitbase reveals that helophytes produce larger seeds than hemicryptophytes (Figure 6, Figure S7; $F = 3.259, df = 620, p = 0.039$ for seed length, and $F = 8.054, df = 536, p < 0.001$ for seed volume) and hydrophytes (Figure 6; $p = 0.007$ for seed volume).

### 4 | DISCUSSION

While seed dispersal is becoming increasingly important in our changing world, little is known about traits and mechanisms regulating seed dispersal by water. Here, we show that in lowland streams, large seeds in general disperse farther than smaller seeds. This effect of seed size on dispersal distance can be explained by the different entrapment mechanisms involved, where net trapping and surface tension more often trap smaller seeds and only wake trapping more frequently entraps larger seeds. Mainly by means of net trapping, in-stream and shoreline vegetation types entrap more smaller than larger seeds and thereby cause the observed positive relation between seed size and dispersal distance. Only the broad-leaved vegetation types, water lily and riparian forbs, are more likely to trap larger than smaller seeds, resulting in a negative relation between seed size and dispersal distance. However, water lilies mainly entrapped seeds through wake trapping. In general, wake trapping occurs infrequently and is only a temporary entrapment mechanism, which is unlikely to affect dispersal distances on the long term.

Furthermore, our study reveals that the entrapment location and, hence, the suitability of this location for germination and survival, may vary with seed size. Not only does denser vegetation entrap more seeds but it also entraps smaller seeds more frequently than larger seeds. We observed no relation between seed size and entrapment by bare sediment, indicating that seeds of all sizes are equally (un)likely to wash up on bare sediment; however, this process is likely to occur at the end of winter/spring flooding periods when water levels drop substantially (Nilsson et al., 2010). In our experiments, we observed minor water-level fluctuations of several cm/day, but these apparently were insufficient for seed deposition at bare sediment. By adding the effects of seed size on entrapment, our findings supplement the few studies that have previously focused on entrapment locations only (Goodson, Gurnell, Angold, & Morrissey, 2003; Nilsson, Andersson, Merritt, & Johansson, 2002; Säumel & Kowarik, 2013; Wolters et al., 2004). A next step would be to use real (spray painted) seeds instead of cork seed mimics to verify our findings and extend the study to investigate effects of other seed characteristics, such as shape, buoyancy, and weight, on dispersal distances.

We demonstrate that seed dispersal distance can vary substantially between streams, seed sizes, and especially seasons (Figure 2), with seed dispersal distances in one stream being >650 times greater than in others (Table S6). Our results indicate that seeds have the potential to disperse over distances as far as 65 km given the proper conditions, such as sufficient open water, low plant densities, and low abundances of finely branched aquatic vegetation (e.g., aquatic grass, floating debris, and starwort). Such conditions predominantly occur during winter, which therefore seems the most important season for long-distance dispersal by water. Studies on seed dispersal and entrapment show that winter is indeed the season in which most seeds are waterborne (Boedeltje, Bakker, Ten Brinke, Van Groenendaal, & Soesbergen, 2004; Gurnell, Boitsidis, Thompson, & Clifford, 2006; Moggridge, Gurnell, & Mountford, 2009).

From an evolutionary perspective, plant species depending on water dispersal may evolve larger seeds to promote long-distance dispersal in flowing water. As many riparian species inhabit dynamic habitats, characterized by frequent disturbances which necessitate frequent (re-)colonization events, large seeds may be expected to be common particularly in this species group. Indeed, our analysis of the LEDA data shows that helophytes tend to have larger seeds than neighbouring hemicryptophytes (which live in more terrestrial sites that are less frequently disturbed and less reachable by water) and hydrocryptophytes (which live in open water and do not require their seeds to be dispersed floating on the water, but rather as bed load; Soons et al., 2017). Long-distance dispersal may be the evolutionary explanation for the large seed sizes of many common helophytes such as Acorus calamus, Iris pseudacorus, and Sparganium species.

One of the main purposes of stream restoration is to increase biodiversity by creating suitable habitat for typical or endangered riparian species (Lake, Bond, & Reich, 2007). Yet, this can only be successful if such species are able to reach these restored areas. Hydrochorous seed dispersal is of key importance for successful colonization of restored rivers and streams (Gurnell et al., 2006; Jansson, Zinko, Merritt, & Nilsson, 2005; Mogggridge et al., 2009). By means of water dispersal, restored river banks are quickly colonized by upstream vegetation (Gurnell et al., 2006). Furthermore, the
number of species colonizing restored sites substantially increases when long-distance seed dispersal via water can occur (Jansson et al., 2005; Vogt, Rasran, & Jensen, 2006; Moggridge et al., 2009). Based on our model calculations, approximately 61% of seeds are likely to be dispersed less than 0.5 km away from their point of entry; and only less than 10% of seeds are likely to disperse further than 5 km. Given that distances between restored stream sections are often larger than this, many plant species may not be able to travel from one restored area to another. Furthermore, entrapment on bare stream banks may pose a problem for colonization in newly restored sites (Riis 2008). For rare or endangered species, this means that they may be unlikely to reach suitable habitat areas in restored streams, and may be unable to colonize these areas successfully. Restoration measures should thus give greater consideration of potential dispersal limitations, particularly in the case of species with small, floating seeds. Importantly, our results suggest that seed dispersal by water would be severely limited if riparian vegetation is mown when seeds are still on the plants in late summer/autumn, as this prevents effective dispersal in winter. Our results also imply that stream management activities and climatic changes, that affect the area of open water and the cover of different vegetation types in and along streams, are very likely to impact the dispersal potential of riparian species that depend on seeds floating on the water surface, and should be further addressed to consolidate our understanding of seed dispersal through nature’s watery veins.

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AUTHORS’ CONTRIBUTIONS

M.d.J. and M.B.S. designed the study; B.K., E.L.J., R.B., and S.G.T.R. collected data; M.d.J. analysed data and wrote the manuscript. All authors contributed to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.10j18k2 (De Jager et al., 2018).

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