Hydrochory and water induced germination enhance invasion of *Fraxinus pennsylvanica*

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A B S T R A C T

In many Central European countries *Fraxinus pennsylvanica* is an invasive species that spreads rapidly in floodplain forests. The aim of this study was to analyse anemochorous and hydrochorous dispersal distances and to compare the findings with dispersal data for the native *Fraxinus excelsior*. A simulation revealed that wind dispersal distances are similar for both species, reaching to 120–250 m. By contrast, the mean floating time (50% floating samaras) measured in an experiment was 2 days in the case of *F. pennsylvanica* and 0.5 days for *F. excelsior*. This high floating ability facilitates water dispersal over several kilometres in both species, but for the invasive species the modelled mean dispersal distance was 3.7 times higher. A germination test of *F. pennsylvanica* seeds revealed that the rate, onset and speed of germination increase with the duration of the inundation. After a maximum storage time in water of about 15 days the germination rate amounts to 78%, which was higher than the germination rate of seeds without storage in water (53%). We also found that regeneration was enhanced in flooded areas. Hydrochory, therefore, may be viewed as an important factor explaining the successful invasion of *F. pennsylvanica* in floodplain forests in Central Europe.

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1. Introduction

The dispersal of samaras by the vector wind is generally assumed to be the most important means of dispersal for *Fraxinus* species as they are morphologically well adapted to wind transport (low weight, samara) (Tackenberg et al., 2003; Hintze et al., 2013). Many *Fraxinus* species, for example, *Fraxinus pennsylvanica* and *Fraxinus excelsior*, grow in floodplain forests where water may also be an important vector for long distance dispersal given the periodic occurrence of floods (Merritt and Wohl, 2002). Stands on these sites are separated by great distances and may be connected by river corridors. Middleton (2000) noted that the fruits of most woody species occurring in floodplain forests are dispersed primarily by water, i.e., hydrochory. Hydrochory is especially important for diversity in floodplain forests (Katenhusen, 2001).

The importance of hydrochory often appears to be high for the dispersal of non-native plant species. Rivers and stream ecosystems frequently possess more non-native species than the surrounding landscape, because of a higher diaspore input brought about by water transport and disturbances caused by water dynamics and floods (Pyšek and Prach, 1993). Water can also be an important secondary dispersal pathway for *F. pennsylvanica*. In European floodplain forests *F. pennsylvanica* is an invasive tree species (Schmiedel, 2010). Its establishment in natural stands leads to the creation of a new biotope type in naturally open areas of floodplain forests. In order to understand the invasion process, it is necessary to obtain information about the dispersal pathways and to compare the dispersal strategy of the species with that of a closely related native tree such as *F. excelsior*. In studying long distance dispersal and plant invasions, less obvious pathways must also be considered (Nathan, 2006; Cain et al., 2000). Especially in *Fraxinus*, a comparison between wind and water dispersal seems necessary. Seed transport by water may be an explanatory factor in the contrasting invasion speeds of different tree species. Thébaud and Debussche (1991), for instance, proved that the rapid spread of *Fraxinus ornus* was due to hydrochory.

First indication about hydrochory in *F. pennsylvanica* and *F. excelsior* was found by Schneider and Sharitz (1988) and Marigo et al. (2000). One of the factors influencing successful dispersal by water that has been widely tested and discussed is seed buoyancy (Schneider and Sharitz, 1988; Danvind and Nilsson, 1997; Boedeltje et al., 2004; Vogt et al., 2004). Buoyancy is an indicator of the potential of a species to be dispersed by water (Knevel et al., 2005).

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After dispersal, seed germination is the next prerequisite for successful establishment. The presence or absence of a species depends not only on the availability of seeds but also on the frequency of 'safe sites' (Harper, 1977). Safe sites are species-specific and have ecosystem-specific risks for germination. On floodplain forest sites the main risks are flood (Kolka et al., 1998; Küßner, 2003) and disturbances such as sedimentation and animal activity. Middleton (2000) emphasised that woody species can only germinate in floodplain forests during the absence of flood and that seedlings mostly die when flooding occurs during the growing period. Water is not only a transportation medium but also influences the germination rate of seeds (Baskin and Baskin, 2001). In the event of flooding, water can also have a negative impact on the viability of the seeds (anaerobic milieu and mechanical stress).

The following questions were posed as part of an investigation of the possibility of the dispersal of *F. pennsylvanica* samaras by means of water and the chances of establishment following hydrochory: Is hydrochory an important dispersal factor for the spread of *F. pennsylvanica* in floodplain forests in Central Europe? How far can samaras float and fly? Of what importance is dispersal by water in comparison to dispersal by wind for this species? Are the seeds tolerant of floods? Is the germination rate influenced negatively by flooding?

2. Materials and methods

2.1. Study species

F. pennsylvanica is widely distributed in the United States and Canada. Its native range extends from Nova Scotia westwards to south-eastern Alberta and southwards through central Montana to south-eastern Texas, Florida and the east coast (Kennedy, 1990). *F. pennsylvanica* is a dioecious tree of 30–40 m in height. The leaves are pinnately compound and 20–30 cm long with 5–9 leaflets. The samaras are 30–55 mm long, 5–8 mm wide and weigh 49.3 mg (standard deviation (SD) 11.7) (Schmiedel, 2010). In its native range, *F. pennsylvanica* can produce fruits every year (Williams and Hanks, 1976), with a mast every 3–5 years (Prasad et al., 2007). *F. pennsylvanica* was introduced to Europe and Germany in the 18th century (Willdenow, 1796), where it was used as an ornamental tree and planted in floodplain forests. The species occurs as an invasive alien tree species regionally, arising in floodplain forests and near waterways (Schmiedel, 2010; Kremer and Čavlović, 2005; Pyšek et al., 2002).

The native range of *F. excelsior* in Europe extends from northeast Spain to western Russia and from southern Norway and Sweden to Italy and Greece. The tree species grows on shallow and dry, calcareous sites as well as on floodplain sites (Roloff and Pietzarka, 1997). *F. excelsior* can reach heights of 40 m and is a trioecious species. Samaras are produced yearly and are 25–50 mm long and 7–11 mm wide (Scheller, 1977). Both ash species have wide ecological amplitudes and can grow on extreme sites.

2.2. Buoyancy experiments

In order to test the floating capacity of samaras of *F. pennsylvanica* in comparison with those of the native *F. excelsior*, a test of buoyancy was run in a laboratory experiment applying the method described by Knevel et al. (2005). The experiment consisted of 400 samaras per species. The samaras selected met the criterion 'externally intact and full.' The *F. pennsylvanica* samaras originated from different trees growing in a floodplain forest along the River Elbe near Dessau in central Germany (Sachsen-Anhalt). The samaras were collected in autumn 2006 and stored dry at 5–8 °C until the time of the experiment (January 2007). The *F. excelsior* samaras

originated from different trees growing in forest seed stands in Sachsen. The samaras of both species were put in 16 glass beakers (10 cm width, 12 cm height, 600 ml volume) and filled with about 300 ml distilled water (Horsch, 2001; van den Broek et al., 2005), corresponding to eight replications with 50 samaras per species. The beakers were placed on a flaskshaker, which moved gently at a frequency of 100 /min and at an amplitude of about 1 cm. The water movement prevented the adherence of the samaras to the glass beakers. The proportion of samaras floating per tree species was captured at progressive time intervals (after 5 min, after 1, 2, 4, 6, 9, 24 and 72 h and after 1 week). The experiment ended after 1 week, when nearly all of the samaras had sunk to the bottom of the beakers. The data were analysed in Origin 8G (OriginLab Corporation, USA). The dependence of buoyancy on time was described using the χ^2 minimisation fitting routine. For the fitting routine, 200 iterations were performed. The best fitting model was selected by evaluating the goodness-of-fit criteria (R^2 and $\chi^2/\mathrm{d}f$ values). R^2 is the adjusted coefficient of determination and $\chi^2/\mathrm{d}f$ represents the magnitude of scattering (χ^2) of observed data and a theoretical curve normalised by a degree of freedom ($\mathrm{d}f$). The time-dependent buoyancy (number of samaras $y(x)$) was described using a four-parameter logistic growth function (dose–response function):

$$y(x) = A_2 + \frac{A_1 - A_2}{1 + \left(\frac{x}{x_0}\right)^p} \tag{1}$$

Parameter A_1 describes the minimum value of the asymptote, A_2 the final value and the parameter p indicates the power of the function. x_0 is the inflexion point of the function and corresponds to the species-specific half-value period when 50% of the samaras have sunk. Accordingly, results were obtained for the two most important parameters: the maximum floating time and the proportion of seeds floating for a certain time period.

2.3. Wind dispersal kernels

The data for the wind dispersal distances of both ash species derived from simulations using the programme PAPPUS (Tackenberg, 2003), which is a process-based seed dispersal model. In the model the plant species are characterised by the terminal velocity of their diaspores (V_{term}: *F. excelsior* = 1.58 m/s; *F. pennsylvanica* = 1.62 m/s) and the height of the infructescence, the 'release height' (H_{rel}: *F. excelsior* = 25 m; *F. pennsylvanica* = 20 m). The wind-vector and turbulence data were measured over a period of 1 year for a low-cut grassland situated within a flat landscape in central Europe (Tackenberg et al., 2003). The wind kernels were first computed for a limited number of combinations of V_{term} and H_{rel}, and the species' kernels were subsequently drawn from these data by means of bilinear interpolation according to the mean terminal velocity and release height. The simulation provided 10,000 distances for each ash species (Hintze et al., 2013).

2.4. Germination after storage in water

To answer the question of whether the germination rate is influenced negatively by flooding, the germination rate of samaras after storage in water was tested. For this experiment, samaras of different *F. pennsylvanica* trees from a stand situated in a floodplain forest along the River Elbe near Dessau in Sachsen-Anhalt were again used. The samaras were collected in autumn 2006 and stored dry at 5–8 °C until spring 2008. Only full seeds were used in the test. The average dimensions of the samaras (mean ± standard deviation) were 45.1 ± 5.5 mm (length) and 5.7 ± 0.9 mm (width). The weights varied between 17 and 92 mg, with a mean of 49.3 ± 11.7 mg ($N = 600$).

The germination rate of *F. pennsylvanica* was tested after 0 (control), 2, 10 and 15 days of storage in water. Every variation of the treatment was tested using three replications with 50 samaras (Baskin and Baskin, 2001). The duration of storage in water was similar to the mean flood times (depending on the altitude) during the vegetation period in the floodplain forest investigated (Klausnitzer and Schmidt, 2002). For the purposes of storing the samaras in water a basin was used for each treatment (diameter = 29 cm; depth = 9 cm), filled with distilled water and kept at room temperature. Distilled water was used to allow for comparability with other studies. The samaras were placed on the surface of the water, sinking over the course of the experiment.

The subsequent germination test followed the ISTA (International Seed Testing Association) guidelines (ISTA, 2005) for ash, namely in a germination box on moist paper and in a germination cabinet with alternating temperatures, 16 h at 20 °C in darkness and 8 h at 30 °C in light. The same temperatures were used successfully for germination tests on *F. pennsylvanica* by Steinbauer (1937) and Bonner (1974). The germination test was terminated after 20 days following the recommendation made by Baskin and Baskin (2001, p. 19).

The data were analysed using Origin 8G and SPSS 11.5. Given the sample size $N = 12$, the critical value $D_{0.05}$ was used for verification (with $N = 12$: 0.375; Sachs, 1997). Significant differences were considered at the $P < 0.05$ level.

A non-linear regression analysis was performed in order to predict the number of germinated seeds as a function of the duration of storage in water. In order to address data obtained for the different variants over time, different fitting models were compared using the χ^2 minimisation fitting routine in Origin 8G. The fitting was based on 200 iterations. The Boltzmann fit was selected as the best fitting model on the basis of an evaluation of the goodness-of-fit criteria (R^2 and χ^2/df values). We used the sigmoidal Boltzmann function with the form:

$$y = A_2 + \frac{A_1 - A_2}{1 + e^{\left(\frac{t - t_0}{d_x}\right)}} \qquad (2)$$

where y describes the number of germinated seeds, A_1 is the start number and A_2 is the final number (maximum number of germinated seeds), t is the time in days, t_0 is the time at which half of the maximum number of seeds has germinated (inflection point of the function) and d_x describes the time constant.

2.5. Regeneration plants in different habitat types

Regeneration plants of *F. pennsylvanica* were analysed in summer 2007 in the Biosphere Reserve Mittlere Elbe in Saxony-Anhalt (Germany). The reserve includes the Elbe River floodplain forests which have a high dominance of this invasive species. The occurrences of more than one regeneration plant were mapped in three forest parts where there was a main appearance of *F. pennsylvanica*. The plants with a height >20 cm were determined by plots of 4 m² (four squares of 1 × 1 m) and allocated four different habitat types: forest (floodplain forest with closed canopy), forest edge (transition between forest and grassland or between forest and forest track), floodway (depression with periodical or permanent flooding) and lane (travelled or untravelled forest tracks and their marginal strip). For all plants we measured the plant height.

3. Results

3.1. Buoyancy of the samaras

The buoyancy differed considerably between the two ash species (Fig. 1 and Table 1). The first *F. excelsior* samaras had already
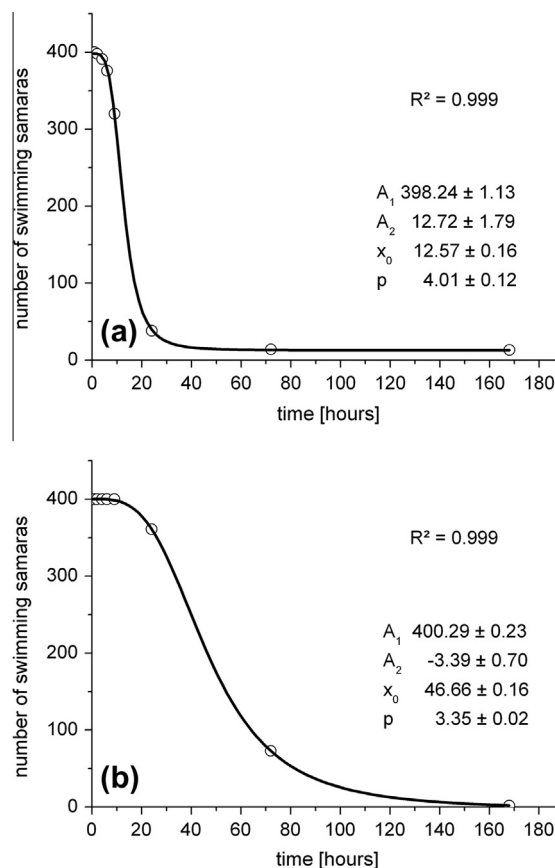

Fig. 1. Measured number of swimming samaras (open circles) and fitting function (logistic growth function) ((a) for *F. excelsior* and (b) for *F. pennsylvanica*).

sunk to the bottom of the beaker after 2 h. After 9 h 80% of the samaras still floated, whereas after 24 h it was only 10%.

By contrast, the first sunken *F. pennsylvanica* samaras were only observed after 24 h (90% still floated). After 3 days 18% of the samaras were still floating. Upon termination of the buoyancy test after one week some samaras of both *F. excelsior* and *F. pennsylvanica* were still floating. No seeds of either of the examined species germinated during the buoyancy test.

The number of sunken samaras plotted against time can reasonably be described for both tree species by a logistic function (Eq. (1)) ($R^2 = 0.999$, $\chi^2/df = 6.395$ for *F. excelsior* and $R^2 = 0.999$, $\chi^2/df = 0.355$ for *F. pennsylvanica*). From this function the half-value period x_0 was calculated. The outcome for *F. excelsior* was 12.6 ± 0.16 h (corresponding to 0.5 days) compared to 46.7 ± 0.16 h (corresponding to 1.9 days) for *F. pennsylvanica*. Accordingly, *F. pennsylvanica* samaras are buoyant an average of four times longer than those of *F. excelsior*.

3.2. Dispersal distances associated with water and wind dispersal

Using the results of the buoyancy test it was possible to estimate dispersal distances for hydrochorous dispersal. Distances were calculated using the fitting function (Eq. (1)) of the buoyancy test and a virtual stream with a mean flow velocity of 3.5 km/h (Fig. 2). This flow velocity is a typical low velocity flow characteristic of European streams. In this example, 50% of the *F. excelsior* samaras were transported over 44 km. The corresponding distance for *F. pennsylvanica* was 163 km, four times longer. Long distance dispersal, in this case the distance 10% of the samaras can float, was 314 km for *F. pennsylvanica* compared to only 76 km for *F. excelsior*.

Table 1
Number and proportion of swimming samaras over time of *F. excelsior* and *F. pennsylvanica* (mean values (MV) of eight replications with standard deviation (SD)).

	0 h	0.08 h	1 h	2 h	4 h	6 h	9 h	24 h	72 h	1 week
Fraxinus excelsior										
MV	100	100	100	99.5	97.75	94	79.9	9.5	3.5	3.25
SD	0	0	0	0.93	2.25	4.0	4.73	3.34	2.56	2.82
Fraxinus pennsylvanica										
MV	100	100	100	100	100	100	100	90.25	18.25	0.5
SD	0	0	0	0	0	0	0	11.68	14.91	0.93
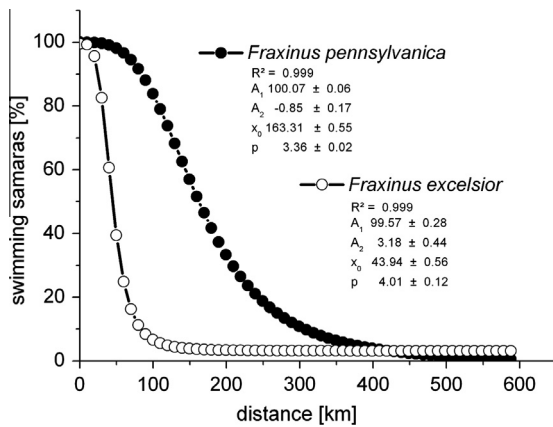
Fig. 2. Fitting function (logistic growth function) for dispersal distances of two ash species of hydrochorous dispersal in a water stream with a mean flow velocity of 3.5 km/h.

Wind dispersal was found to be less efficient. According to our simulation, most seeds are probably to be dispersed less than 100 m of the mother plant (Fig. 3) and the maximum dispersal distance was less than 250 m in both species (N = 10,000 trajectories).

3.3. Germination rate after storage in water

No *F. pennsylvanica* seeds germinated during the storage in water. The mean germination rate of the seeds without storage in water (control) amounted to 52.67% (SD 6.11). The germination rate clearly increased with the length of the period of storage in water (see Fig. 4, R^2 = 0.82 ($P < 0.01$)).

To compare the timing of the onset of germination and the process, the cumulative number of germinated seeds in the three variants corresponding to different durations of storage in water were plotted against time (Fig. 5). The seeds in the control exhibited a delayed onset of germination, which only began after 5 days. The storage of seeds in water for 2 days accelerates the onset of germination by 2 days. Longer storage of the seeds in water effected only a marginal acceleration of germination compared to the variant involving 2 days storage in water. The maximum number of germinated seeds was attained in every variant after 12 days.

The Boltzmann fits for the germination response of the four variants over time revealed a high goodness-of-fit (R^2 = 0.99) (Fig. 5). The parameters of the function are shown in Table 2. A longer duration of storage in water accelerated the germination process in the three variants, expressed in a steeper slope of the fitting curve. The germination rate and the slopes of the curves of the four variants can be ordered as follows: 15 days > 10 days > 2 days > control.

3.4. Establishment of regeneration in different habitat types

We determined regeneration plants in 42 plots. 40% (16) of all plots are floodways and they include the most plant individuals
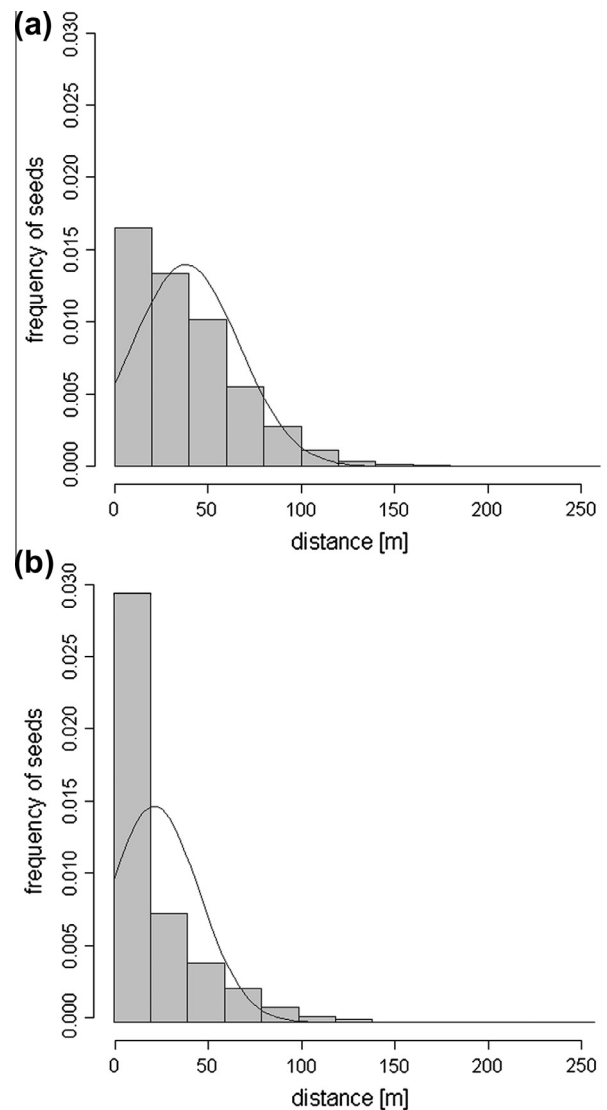
Fig. 3. Modelled distance kernels for wind dispersal for both tree species ((a) *F. excelsior* and (b) *F. pennsylvanica*).

(52%) (Fig. 6). 12 plots were allocated to the habitat type forest (29%), but only 11% of plants individuals were counted there. The density of plants in forest plots (mean = 1.7 plants/m²; SD = 2.3) is significantly lower than in the other plots ($p < 0.001$). The population density in floodways amounts to 5.8 plants/m². Plants of *F. pennsylvanica* in forest plots also represent significant lower heights (mean = 41.0 cm; SD = 22.2) than the plants in the other three habitats ($p < 0.001$). The mean height of the other habitat types amounts to: lane 43.3 cm, floodway 51.2 cm, forest edge 55.3 cm.
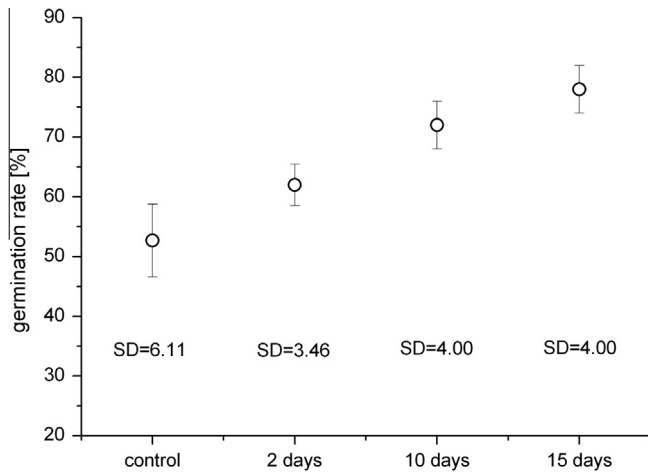
Fig. 4. Germination rate (mean ± SD) of *F. pennsylvanica* seeds after a storage in water of 2, 10, and 15 days, and without water storage (control) including three replications each 50 seeds. The mean values of the germination rates amount for the control 53%, for 2 days storage in water 62.00%, for 10 days 72.00% and for 15 days 78.00%.
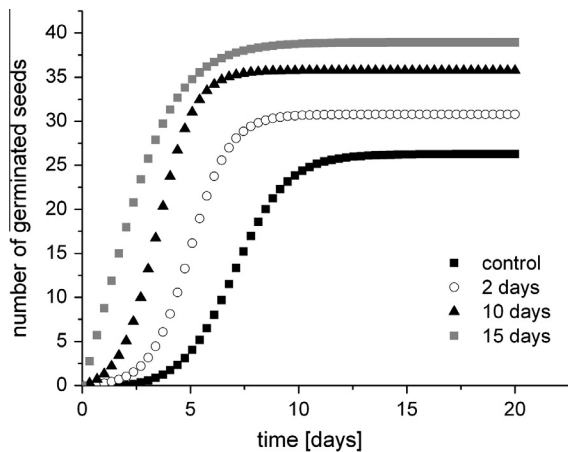

Fig. 6. *Fraxinus pennsylvanica* regeneration in four different habitat types and their abundance.

Fig. 5. Number of germinated seeds for no (control) and three different variants of storage in water (Boltzmann fit, parameters see Table 2).

4. Discussion

4.1. Hydrochorous dispersal

The buoyancy test confirmed that the samaras of *F. pennsylvanica* and *F. excelsior* are buoyant and may be dispersed by water over distances of several kilometres. Evidence of hydrochorous dispersal in *F. pennsylvanica* was demonstrated previously by Wilson (1980), Schneider and Sharitz (1988) and Middleton (2000). In an experimental approach Schaffrath (2001) showed that *F. pennsylvanica* samaras can float for between 2 and 10 days, a finding
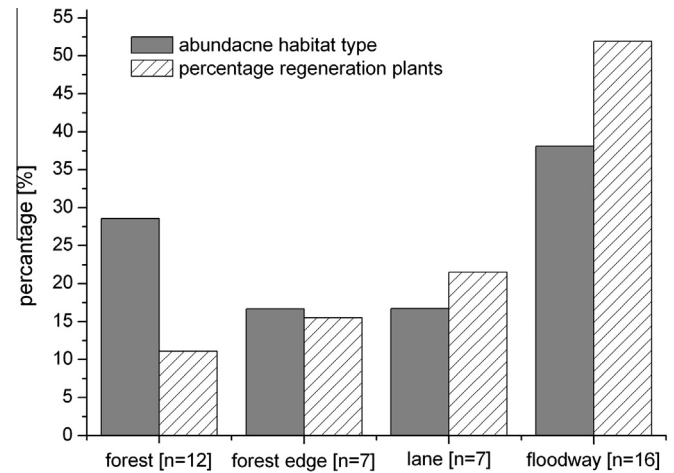
similar to the results presented here. By contrast, the samaras of *F. excelsior* float for shorter periods. Praeger (1913), for example, observed three days. This is roughly in accordance with our results, where the samaras sunk slightly faster.

The presence of flowing water (rivers) or periodic flowing water (floods) gives rise to the possibility of secondary dispersal of seeds by means of water (Horsch, 2001; Vogt et al., 2004; Säumel and Kowarik, 2010). It is necessary to mention, however, that under natural conditions buoyancy may be shorter than was observed under laboratory conditions, as factors such as strong wave movements and rain may reduce buoyancy (Merritt and Wohl, 2002). Results of other studies show that seed buoyancy is not responsible for plant distribution in floodplain ecosystems, species with low floating ability can also be transported over long distances (Danvind and Nilsson, 1997; Andersson et al., 2000). Other factors of dispersal and establishment should be considered. Leyer and Pross (2009) remark that dispersal processes seem to work effectively only by the movements of floods and that these conditions can compensate low seed buoyancies. Nevertheless, the enhanced transport of samaras via water results in a greater chance of establishment (van den Broek et al., 2005).

The tests revealed considerable differences between the buoyancy of the samaras of the native and those of the invasive ash species. Accordingly, *F. pennsylvanica* has a higher potential for hydrochorous dispersal but dispersal distances depend on the flow velocity of the water. By contrast, the wind dispersal distances for both ash species according to our simulation are very similar and amount to only a few hundred metres (in the simulations: < 250 m). Comparable results for seed dispersal distances by wind in a floodplain forest are shown by Schmiedel (2010) (LDD 150 m). Dispersal by small mammals or birds is also possible (Crowder and Harmsen, 1998). Large dispersal distances with these vectors are expected but unpredictable (Nathan et al., 2008) and maximum dispersal distances are highly stochastic (Soons et al., 2004).

From the results, we conclude that water dispersal is the most important dispersal vector for long distance dispersal in both

Table 2
Results of the Boltzmann fit for the germination test. A_1, A_2, t_0 and d_x are parameters of the function, R^2 is the coefficient of determination and χ^2/df represents the magnitude of scattering of experimental data points over a fitting curve normalised by degree of freedom (df).

	A_1	A_2	t_0	d_x	R^2	χ^2/df
Control	−0.37 ± 0.21	26.25 ± 0.19	7.04 ± 0.11	1.21 ± 0.11	0.99	0.10
2 days	−0.13 ± 0.34	30.77 ± 0.16	4.99 ± 0.15	0.91 ± 0.06	0.99	0.10
10 days	−0.61 ± 0.39	35.76 ± 0.16	3.47 ± 0.04	0.85 ± 0.05	0.99	0.10
15 days	−17.27 ± 4.67	38.94 ± 0.08	1.24 ± 0.33	1.53 ± 0.10	0.99	0.02

species and specifically supports the spread of the invasive species. Similarly, the establishment of *F. ornus* in southern France is facilitated by hydrochory (Thébaud and Debussche, 1991). Populations of this species may spread at a rate of 970 m per year. Kremer and Čavlović (2005) assumed that the spread of *F. pennsylvanica* in the Danube floodplains in Croatia was mainly caused by hydrochorous dispersal of samaras during flooding. Schaffrath (2001) mentioned that in the Oder floodplain (Brandenburg) regeneration of *F. pennsylvanica* can be observed along rivers (e.g., the River Oder, Oder-Spree Canal) many kilometres away from seed trees. We assume that this pattern can only be explained by hydrochory, because the distances involved are too great for wind dispersal. The rapid spread of *F. pennsylvanica* may, therefore, be expected in floodplains (Schmiedel, 2010), as could also be shown by the results of the studied regeneration plants in floodways. *F. pennsylvanica* can grow in varied environments, but the establishment depends on high light requirement in the seedling phase (Küßner, 2003). Regeneration plants of *F. pennsylvanica* are very well adapted on flooding conditions (Hook and Brown, 1973; Walls et al., 2005).

4.2. Germination after storage in water

The test of the germination rate of *F. pennsylvanica* samaras after different durations of storage in water provided an estimate of the potential extent of seedling establishment after hydrochorous seed dispersal. The results revealed a germination rate for *F. pennsylvanica* in the control variant of about 53%. The onset of germination was accelerated as a consequence of storage in water. Walls et al. (2005) observed a delay of germination in an experiment involving static and periodic flooding in a pot. This demonstrates the germination process of *F. pennsylvanica* under flooding conditions but not the germination capacity after hydrochorous dispersal. A longer duration of storage in water elevated the germination rate in the present study. This statement is also in agreement with DuBarry (1963), but in that study the germination rate amounts to 30% after 30 days stratification and after an additional 30 days storage in water 5 cm deep. The experiments by Walls et al. (2005) revealed that flooding resulted in no significant differences in the total germination rate (80% for all treatments). Bonner (1974) documented a germination rate of approximately 70% over a period of 20 days for *F. pennsylvanica* seeds that had been stratified but not stored in water. However, in our study, correspondingly high germination rates were observed in the variants involving only 10 and 15 days storage in water. Taylor (1972) observed similar germination rates after the stratification of *F. pennsylvanica* seeds, based on germination tests carried out under greenhouse conditions, which produced mean germination rates of around 60%. It is apparent that the germination rate in *F. pennsylvanica* varies considerably because of different experimental methods but that water has a considerable influence on the germination success.

F. pennsylvanica is a tree species with a soft seed coat (nitrogen-free extract > 28, DuBarry, 1963) and water is expected to have a beneficial impact on germination. Marshall (1981) tested different possibilities to break the dormancy of *F. pennsylvanica* seeds, one of which was found to be storage in water. Kennedy (1990) also identified storage in water as a dormancy breaker. The results obtained in the study presented revealed a germination rate of 78% after 15 days storage. Caixia and Rongfu (1991) verified that the endosperm and pericarp of *F. pennsylvanica* contain abscisic acid (ABA). In a situation with sufficient water supply, as demonstrated by the storage of *F. pennsylvanica* seeds in water, the ABA content declines. This is one possible reason for the rapid germination after storage in water. Experiments to ascertain the ABA content of seeds during storage in water failed. Sutherland et al. (2000) demonstrated that *F. pennsylvanica* seeds require a moist seed bed. This explains the better germination rate after storage in water and highlights the clear dependency of seeds on water availability. The germination rate of *F. pennsylvanica* after a period of storage in water longer than the investigated 15 days is unknown.

5. Conclusions

The dispersal of seeds by water can provide additional colonising opportunities for invasive species that are primarily wind dispersed. The results of the study demonstrated that the samaras of *F. pennsylvanica* are buoyant and flood tolerant over several days, thereby facilitating hydrochorous dispersal over distances of several kilometres. It can be shown that water as dormancy breaker for the seeds of *F. pennsylvanica* in combination with hydrochorous dispersal is responsible for a possible higher probability for range expansion of this invasive species. By contrast, wind dispersal distances are considerably smaller in both *F. pennsylvanica* and in the native ash species *F. excelsior*. From this, we conclude that in flooded areas water is the most important medium for the spread of *F. pennsylvanica* over long distances. Accordingly, the species has the potential to spread rapidly along rivers and so the further invasion of floodplain forests by *F. pennsylvanica* must be anticipated.

It is necessary to analyse the establishment of seedlings in new areas in order to assess the relative importance for the further spread of the species of dispersal vs. recruitment ability (e.g., Oester et al., 2009). Prevention management should focus on sites with hydrochorous dispersal paths and high conservation values.

References

Andersson, E., Nilsson, C., Johansson, M.E., 2000. Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. J. Biogeogr. 27, 1095–1106.

Baskin, C.C., Baskin, J.M., 2001. Seeds, Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, San Diego.

Boedeltje, G., Bakker, J.P., Brinke, A.T., van Groenendael, J.M., Soesbergen, M., 2004. Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. J. Ecol. 92, 786–796.

Bonner, F.T., 1974. *Fraxinus* ash. In: Schopmeyer, C.S. (tech. coord.), Seeds of woody plants of the United States. Agriculture handbook 450. US Department of Agriculture, Washington DC, pp. 411–416.

Cain, M.L., Milligan, B.G., Strand, A.E., 2000. Long-distance seed dispersal in plant populations. Am. J. Bot. 87, 1217–1227.

Caixia, Z., Rongfu, G., 1991. Effect of ABA and other endogenous inhibitors on *Fraxinus pennsylvanica* Marsh. J. Beijing Forestry Univ. (China) 13, 39–46.

Crowder, A., Harmsen, R., 1998. Notes on forest succession in old fields in southeastern Ontario: the woody species. Canadian Field-Naturalist. 112, 410–418.

Danvind, M., Nilsson, C., 1997. Seed floating ability and distribution of alpine plants along a northern Swedish river. J. Veg. Sci. 8, 271–276.

DuBarry Jr., A.P., 1963. Germination of bottomland tree seed while immersed in water. J. For. 61, 225–226.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, New York–London–San Francisco.

Hintze, C., Heydel, F., Hoppe, C., Cunze, S., König, A., Tackenberg, O., 2013. D[3]: The dispersal and diaspore database – baseline data and statistics on seed dispersal. Perspect. Plant Ecol. Evol. Syst. 15, 180–192.

Hook, D.D., Brown, C.L., 1973. Root adaptations and relative flood tolerance of five hardwood species. For. Sci. 19, 225–229.

Horsch, M., 2001. Experimentelle Ausbreitungsbiologie bei Primulaceen. Dissertationes Botanicae Bd. 341.

ISTA, 2005. Internationale Vorschriften für die Prüfung von Saatgut. Bassersdorf (CH). p. 29.

Katenhusen, O., 2001. Die Ausbreitung von Pflanzen durch Hochwasser in norddeutschen Flusslandschaften. Z. Ökologie u. Naturschutz 9, 225–236.

Kennedy, H.E. Jr., 1990. *Fraxinus pennsylvanica* Marsh. Green ash. In: Burns, R.M., Honkala, B.H. (techn. coord.), Silvics of North America. vol. 2. Hardwoods. Agriculture handbook. 654. US Department of Agriculture, Washington DC, pp. 348–354.

Klausnitzer, U., Schmidt, P.A., 2002. Vegetationskundliche Charakterisierung von Waldbeständen auf Hartholz-auenstandorten. In: Roloff, A., Bonn, S. (Eds.), Ergebnisse ökologischer Forschung zur nachhaltigen Bewirtschaftung von Auenwäldern an der Mittleren Elbe. Forstwiss. Beitr. Tharandt/Contrib. For. Sci. 17, pp. 123–154.

Knevel, I.C., Bekker, R.M., Kunzmann, D., Stadler, M., Thompson, K. (Eds.), 2005. The LEDA traitbase collecting and measuring standards. Life-history traits of the northwest European flora.

Kolka, R.K., Trettin, C.C., Nelson, E.A., Conner, W.H., 1998. Tree seedlings establishment across a hydrologic gradient in a bottomland restoration. In: Cannizzaro, P.J. (Eds.), Proceedings of The Twenty Fifth Annual Conference on Ecosystems Restoration and Creation, May 1998, pp. 89–102.

Kremer, D., Čavlović, J., 2005. Distribution of introduced North American ash species and their role in lowland forest management in Croatia. J. For. 103, 309–313.

Küßner, R., 2003. Mortality patterns of *Quercus*, *Tilia* and *Fraxinus* germinants in a floodplain forest on the river Elbe, Germany. For. Ecol. Manage. 173, 37–48.

Leyer, I., Pross, S., 2009. Do seed and germination traits determine plant distribution patterns in riparian landscapes? Basic Appl. Ecol. 10, 113–121.

Marigo, G., Peltier, J.-P., Girel, J., Pautou, G., 2000. Success in the demographic expansion of *Fraxinus excelsior* L. Trees 15, 1–13.

Marshall, P.E., 1981. Methods for stimulating green ash seed germination. Tree planters' notes, summer, pp. 9–11.

Merritt, D.M., Wohl, E.E., 2002. Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. Ecol. Appl. 12, 1071–1087.

Middleton, B., 2000. Hydrochory, seed banks, and regeneration dynamics along the landscape boundaries of a forested wetland. Plant Ecol. 146, 169–184.

Nathan, R., 2006. Long-distance dispersal of plants. Science 313, 786–788.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A., Tsoar, A., 2008. Mechanisms of long-distance seed dispersal. Trends Ecol. Evol. 23, 638–647.

Oester, M., Ask, K., Römermann, C., Tackenberg, O., Eriksson, O., 2009. Plant colonization of ex-arable fields from adjacent species-rich grasslands: the importance of dispersal vs. recruitment ability. Agric. Ecosyst. Environ. 130, 93–99.

Praeger, R.L., 1913. On the buoyancy of the seeds of some Britannic plants. Scientific Proc. Royal Dublin Society 14, 13–62.

Prasad, A.M., Iverson, L.R., Matthews, S., Peters, M., 2007–ongoing. A climate change atlas for 134 forest tree species of the eastern United States [database]. , Northern Research Station, USDA Forest Service, Delaware, Ohio. <http:// www.nrs.fs.fed.us/atlas/tree> (accessed 12.11.12).

Pyšek, P., Prach, K., 1993. Plant invasions and the role of riparian habitats: a comparison of four species alien to central Europe. J. Biogeogr. 20, 413–420.

Pyšek, P., Sádlo, J., Mandák, B., 2002. Catalogue of alien plants of the Czech Republic. Preslia 74, 97–186.

Roloff, A., Pietzarka, U., 1997. *Fraxinus excelsior* L. (Gemeine Esche). In: Schütt, P., Schuck, H.J., Lang, U.M., Roloff, A. (Eds.): Enzyklopädie der Holzgewächse 3, pp. 1–15.

Sachs, L., 1997. Angewandte Statistik. Anwendung statistischer Methoden. 8. Aufl. Springer Verlag, Berlin Heidelberg.

Säumel, I., Kowarik, I., 2010. Urban rivers as dispersal corridors for primarily wind-dispersed invasive tree species. Landsc. Urban Plan. 94, 244–249.

Schaffrath, J., 2001. Vorkommen und spontane Ausbreitung der Rotesche (*Fraxinus pennsylvanica* Marshall) in Ost-Brandenburg. Nat.schutz Landsch.pfl. Brandenbg. 10, 134–139.

Scheller, H., 1977. Kritische Studien über die kultivierten *Fraxinus*-Arten. Mitt. Dtsch. Dendrol. Ges. 69, 49–162.

Schmiedel, D., 2010. *Fraxinus pennsylvanica* Marsh. in den Auenwäldern der Mittelelbe. Invasionsbiologie und ökologisches Verhalten im naturschutzfachlichen Kontext. Berliner Beiträge zur Ökologie Band 6. Weißensee Verlag, Berlin.

Schneider, R.L., Sharitz, R.R., 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. Ecology 69, 1055–1063.

Soons, M.B., Nathan, R., Katul, G.G., 2004. Human effects on long-distance wind dispersal and colonization by grassland plants. Ecology 85, 3069–3079.

Steinbauer, G.P., 1937. Dormancy and germination of *Fraxinus* seeds. Plant Physiol. 12, 813–824.

Sutherland, E.K., Hale, B.J., Hix, D.M., 2000. Defining species guilds in the Central Hardwood forest, USA. Plant Ecol. 147, 1–19.

Tackenberg, O., 2003. Modeling long-distance dispersal of plant diaspores by wind. Ecol. Monogr. 73, 173–189.

Tackenberg, O., Poschlod, P., Bonn, S., 2003. Assessment of wind dispersal potential in plant species. Ecol. Monogr. 73, 191–205.

Taylor, S.M.O., 1972. Ecological and genetic isolation of *Fraxinus americana* and *Fraxinus pennsylvanica*. University of Michigan, Dissertation.

Thébaud, C., Debussche, M., 1991. Rapid invasion of *Fraxinus ornus* L. along the Hérault River system in southern France: the importance of seed dispersal by water. J. Biogeogr. 18, 7–12.

van den Broek, T., van Diggelen, R., Bobbink, R., 2005. Variation in seed buoyancy of species in wetland ecosystems with different flooding dynamics. J. Veg. Sci. 16, 579–586.

Vogt, K., Rasran, L., Jensen, K., 2004. Water-borne seed transport and seed deposition during flooding in a small river-valley in northern Germany. Flora 199, 377–388.

Walls, R.L., Wardrop, D.H., Brooks, R.P., 2005. The impact of experimental sedimentation and flooding on the growth and germination of floodplain trees. Plant Ecol. 176, 203–213.

Willdenow, C.L., 1796. Berlinische Baumzucht. Berlin.

Williams, R.D., Hanks, S.H., 1976. Hardwood nurseryman's guide. Agric. Handb. 473. USDA For Serv Washington, DC.

Wilson Jr., R.G., 1980. Dissemination of weeds by irrigation water. Weed Sci. 28, 87–92.