Hydrology, shore morphology and species traits affect seed dispersal, germination and community assembly in shoreline plant communities

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Summary

1. Seed dispersal and germination are two primary processes influencing plant community assembly. On freshwater shores, water levels regulate both processes. However, it is still unclear how water levels, shore morphology and species traits interactively affect seed dispersal and germination, and how these interactions determine plant community assembly. We hypothesize that a drawdown water regime enhances seed establishment compared to a year-round stable water level, that this increases species richness and diversity, and that this is modulated by species traits and shore morphology.

2. Germination of 20 wetland plant species with different dispersal capacities (floating capacity expressed as seed floatation half-time) and soil moisture preferences for germination (Ellenberg F) was tested on artificial shores in 24 outdoor ponds in two complementary experiments over 8 weeks. The 'dispersal experiment' tested the effect of water regime on recruitment of hydrochorously dispersing seeds. The 'seed bank experiment' tested the effect of water regime on germination from a sown seed bank, on steep and gradual shores.

3. In the dispersal experiment, the drawdown regime increased recruitment and species richness. Longer floating species colonized a larger shoreline section. Soil moisture preference for germination did not determine colonization patterns.

4. In the seed bank experiment, the drawdown regime increased the number of seedlings on gradual sloping shores, but not on steep shores. The number of germinating seedlings corresponded to the area subjected to the drawdown regime in both shore types. Species richness was not affected by water regime or shore morphology, and species traits did not determine shoreline colonization. Most seeds germinated in moist soil conditions for all species.

5. *Synthesis.* A spring drawdown instead of stable water regime stimulates establishment of hydrochorously dispersing seeds in temperate wetlands, leading to higher species richness and diversity. Germination from the seed bank is more affected by water regime and shore surface than by the tested species traits. Species traits, water levels and shore morphology together determine wetland plant community assembly, with dispersal as the main driver of seedling community diversity. Water-level regulations and shore morphology can be used to influence plant communities in wetland restoration.

Key-words: biodiversity, determinants of plant community diversity and structure, Ellenberg, hydrochory, river, seed floatation, shore slope, soil moisture preference, wetland, zonation

Introduction

Propagule dispersal to suitable habitat and subsequent germination are two primary processes influencing plant community structure (Grubb 1977; Nilsson *et al.* 2010). Establishment of plants from mobile seeds can secure the future of the existing communities in changing environments (Kalamees & Zobel 2002) or increase species richness by introducing new species (Tilman 1997; Foster 2001; Jansson *et al.* 2005). Although many plants can reproduce clonally and spread to a new habitat without seed production (Grace 1993; Pan & Price 2001), recruitment of seeds still remains important. This is illustrated by the current decline of plant species richness in Northwest Europe, which has partly been attributed to a reduction in seed mobility and establishment (Ozinga *et al.* 2009; Brederveld *et al.* 2011). This decline is especially evident for plants relying on hydrochorously (water-) dispersed seeds on freshwater shores (Ozinga *et al.* 2009). The habitat on the boundary between water and land harbours a relatively high number of plant species (Nilsson & Svedmark 2002; Sabo *et al.* 2005).

For shore vegetation, water is a highly important dispersal vector (for review see Nilsson *et al.* 2010). Previous field experiments have shown that water dispersal contributes strongly to the establishment of pioneer vegetation on shores (Jansson *et al.* 2005; Leyer 2006; Merritt, Nilsson & Jansson 2010). Many wetland plant seeds have impermeable coats, air-filled cavities, or other traits that enhance their floatation and therewith their dispersal by water (Boedeltje *et al.* 2003). After arrival in a suitable habitat, water levels additionally determine soil moisture conditions and thereby affect the germination potential of both newly dispersed seeds and seeds already present in the soil seed bank (Casanova & Brock 2000; Boedeltje, ter Heerdt & Bakker 2002). Water levels and fluctuations in ponds and rivers are therefore considered major regulators of seed dispersal and establishment, and therewith the ultimate community assembly on shores (Greet, Angus Webb & Cousens 2011). Flow regimes modulate seed dispersal by water and can therewith facilitate directed dispersal to particular sections on the shore (Merritt & Wohl 2002). Under more lentic conditions, species traits such as floating capacity become especially important for this stranding process (Andersson, Nilsson & Johansson 2000). However, how species traits and shore morphology interactively affect seed dispersal and germination, and therewith the ultimate species community that establishes on shores, is still unresolved.

With increasing regulation of water levels, the hydrology of many wetlands nowadays changes from a natural fluctuating regime that depends on rainfall and evaporation (mostly resulting in drawdown over summer in temperate regions) to a stable water regime year-round (Kingsford 2000; Lamers, Smolders & Roelofs 2002; Elderd 2003; Raulings *et al.* 2011; Ström, Jansson & Nilsson 2012). Increased water-level regulation is known to affect many aspects of aquatic systems (Bunn & Arthington 2002). This includes plant diversity on the shore, as temporary drying of ponds and fluctuating water regimes alter both plant abundance and species richness (Jansson *et al.* 2005; Van Geest *et al.* 2005; Nilsson *et al.* 2010; Raulings *et al.* 2010).

However, to what extent seed dispersal and germination are mechanisms contributing to the observed effects by interacting with species traits has received relatively little attention.

Seed floatation capacity and soil moisture preference for growth may predominantly determine where seeds arrive and germinate (Coops, van den Brink & van der Velde 1996; Nygaard & Ejrnaes 2009; Geissler & Gzik 2010). If so, the frequently observed zonation of wetland plant communities, whereby each plant species occupies a certain section of the shore, may already be determined at the seedling stage (Coops & van der Velde 1995). On the other hand, others argue that most wetland plants prefer similar germination conditions, that is, moist but not flooded sediment (Boedeltje, ter Heerdt & Bakker 2002). The observed zonation may in that case be due to processes after the initial establishment phase: for instance due to adaptations in later life stages (Blom & Voesenek 1996), due to interspecific competition for light and nutrients with established vegetation, or due to competition between seedlings (Parolin 2001; Kotowski *et al.* 2006; Engels, Rink & Jensen 2011). We designed a mesocosm experiment to test the effect of species traits and environmental conditions on the initial assembly of seedling communities, and took into account an often-overlooked component of freshwater shores: shore morphology.

The effect of water levels on plant community assembly interacts strongly with the shore morphology, as the slope of the shore determines the area of soil surface affected by fluctuations in the water level. However, most glasshouse experiments until now have compared germination under different water-level treatments in containers with flat soils (excluding a slope). There is still little known on the importance of shore slopes in relation to water-level fluctuations. A slope creates a spatial gradient in soil moisture conditions, and the angle of the slope determines the extent of the shore influenced by the water level, which may affect both the arrival of hydrochorously dispersed seeds and local germination conditions.

In this study, we test the interactive effects of water level, species traits and shore morphology on the dispersal and germination of seeds and the assembly of the resulting seedling community. We performed two complementary experiments with a selection of 20 wetland plant species representing a range of traits. In the first experiment, that is, the dispersal experiment, we released seeds in the water in early spring and monitored their establishment on the shore under different water regimes. This allowed us to compare seed dispersal and subsequent germination between a stable and drawdown water regime. We tested how the ultimate plant community assembly was determined by the species traits 'seed floatation capacity' (measured as duration before sinking expressed as the floatation duration half-time according to the LEDA trait data base, Kleyer *et al.* 2008) and 'habitat preference for moisture' (indicated by 'Ellenberg value', an indicator value for plant soil moisture preference, Ellenberg *et al.* 1992; Diekmann 2003). In the second experiment, that is, the seed bank experiment, we specifically asked how germination from the seed bank is affected by the water regime, and how this interacts with shore morphology and species traits.

For both experiments, we hypothesized that (i) a water drawdown regime over six weeks during spring will improve soil moisture conditions for germination of both dispersing and seed bank seeds compared to a stable water regime, leading to a higher germination percentage and diversity of germinating seeds and (ii) species traits (Ellenberg moisture value and seed floatation) determine where seedlings establish on the shore, leading to zonation in the plant community already during the seedling stage. For the seed bank experiment, we specifically hypothesized that the water regime interacts with the morphology of the shoreline. If shores provide more space with suitable germination conditions for seeds to germinate, this will lead to a proportionally higher number and higher diversity of germinating seedlings.

Materials and methods

EXPERIMENTAL DESIGN

Two complementary experiments were performed in 24 outdoor experimental ponds at Loenderveen (52°12′ N, 5°02′ E, the Netherlands); 12 ponds were used per experiment. The first experiment was designed to test the effect of water-level drawdown on the dispersal and subsequent germination of seeds on the shore, for which seeds were released in the water (the dispersal experiment). In the second experiment, the effect of water-level drawdown on seeds in the soil seed bank on the shore was tested, including the effects of shore morphology (the seed bank experiment). Both experiments lasted 8 weeks, as they were aimed at testing the initial establishment and assembly of the seedling community without effects of competition. The experiment ran from 17 April 2012 to 14 June 2012.

The experimental ponds were 5×5 m wide at the top and 3×3 m at the bottom, 1.5 m deep and lined with waterproof foil. The sides of all ponds had a slope of 45°. The ponds were filled with a sediment layer of 0.3 m (a mixture of sand and clay, 10:1), and water from a nearby lake ('Waterleidingplas'). Phosphate had been actively removed from the water by a drinking water supply company, but the water had a high calcium content (pH 8.3, 4.43 µg L^{-1} NO_2, 6.04 µg L^{-1} NO_3, with NH_4^+ and PO_4^{3-} below the detection limit of 7 µg L^{-1}, measured after stabilization in the ponds). We installed two water regimes: one 'stable regime' with a water level 0.5 m above the sediment and one 'drawdown regime' where the water-table was lowered 5 cm each week during 6 weeks (from 0.65 to 0.35 m above the sediment). The water level in all ponds was regulated by overflow mechanisms consisting of a 0.07-m-diameter pipe covered with a 0.2 mm mesh, thus allowing excess overflow of precipitation while preventing loss of floating seeds. There was no movement of the water, except if induced by wind, thus representing ponds and lakes or slow flowing riparian zones of rivers. Water loss by evaporation was replaced with water from the same source on a weekly basis (with an average of 0.02 m, range 0–0.05 m). In the 'drawdown regime', the overflow pipe (also covered with mesh) was lowered each week to 5 cm below the level of the previous week. After 6 weeks of drawdown regime, the water level was kept constant until after a total of 8 weeks both experiments were terminated to avoid the influence of processes other than seed establishment (Engels, Rink & Jensen 2011). To avoid seed predation by birds, all ponds were covered with nets (maze width: 0.025 m), reducing ambient light conditions by < 10%. No fish or macrophytes were present in the ponds. Twenty wetland plant species were selected representing different seed floatation and soil moisture preferences (expressed by Ellenberg moisture index, Ellenberg *et al.* 1992; see Table 1 for the species list). Seeds were obtained from suppliers indicated in Table 1.

Table 1. The 20 plant species used in the experiments with their traits: seed weight in mg (based on mean of 40 seeds), the origin of the seeds (1: Jelitto Staudensamen GmbH, Schwarmstedt, Germany, 2: Cruydt-Hoeck, Nijeberkoop, the Netherlands, 3: seeds collected ourselves in Dutch fens in 2011, 4: B & T World Seeds, Aigues-Vives, France), the number of seeds released during the dispersal experiment and sown per mat during the seed bank experiment (0.5 g), the Ellenberg value for soil moisture [classes are taken from the literature, whereby classes 1–3 are plants generally living in dry to very dry habitat, classes 4–6 in dry to moist habitat, 7–9 in moist to wet habitat and 10–12 in wet or submerged habitat, for more details see: Ellenberg *et al.* (1992)] and the plant life form according to the LEDA trait data base (Kleyer *et al.* 2008): C = chamaephyte, G = non-bulbous geophyte, H = hydrophyte, Hc = hemicryptophyte. All species were perennial

Species	Origin of seeds	Seed weight (mg)	No. of seeds in 0.5 g	Ellenberg value	Life form
Alisma plantago-aquatica	1	0.22	2317	10	H
Butomus umbellatus	1	0.17	2946	10	H
Calla palustris	1	3.28	153	9	H/G
Caltha palustris	1	0.55	915	9	Hc
Carex pseudocyperus	2	0.62	812	9	Hc/H
Carex vulpina	1	1.14	439	8	Hc/G
Eupatorium cannabinum	1	0.23	2202	7	Hc
Filipendula ulmaria	1	0.54	924	8	Hc
Glyceria maxima	1	0.72	697	10	H
Hierochloe odorata	1	0.56	890	9	Hc
Holcus lanatus	2	0.38	1322	6	Hc
Hypericum perforatum	1	0.1	4817	4	Hc/C
Lychnis flos-cuculi	1	0.14	3471	7	Hc
Lycopus europaeus	2	0.24	2123	9	Hc
Lythrum salicaria	1	0.04	12829	8	Hc
Mentha aquatica	1	0.16	3032	9	H
Rumex hydrolapathum	3	4.43	113	10	Hc/H
Stachys palustris	2	0.69	724	7	G
Urtica dioica	4	0.12	4103	6	Hc
Veronica beccabunga	2	0.05	10157	10	Hc/H

To monitor seed establishment, artificial shores were created from Astroturf mats (0.9 m long and 0.5 m wide; AstroTurf® Classic Mat & Classic Roll, Dalton, Georgia, USA; *sensu* Wolters *et al.* 2004). The mats were filled with 10 L potting soil per mat (dry matter 30%, organic matter 17%, NPK 14–16–18 = 1.2 kg m^{-3} and resin-coated fertilizer with NPK 18–6–12 = 1 kg m^{-3}, free of seeds) and assembled partly submerged on the side of the ponds, at either a steep (45°) or gradual (30°) angle with the water level depending on the experiment. At the stable water regime treatment, all mats were submerged for 0.45 m of their length. At the drawdown regime, the mats were initially submerged for 0.8 m of their length, of which *c.* 0.07 m of the steep mats and 0.10 m of the gradual mats were exposed per week due to the lowering of the water level. This led to a total exposure of 0.42 m length and 0.21 m^2 surface of the steep mats, and 0.60 m and 0.30 m^2 of the gradual mats over the total experiment. To determine the position of seedlings on the mats, each mat was divided into nine horizontal sections of each 0.1 m length, and individual seedlings were counted per section.

DISPERSAL EXPERIMENT

For the dispersal experiment, four mats were attached per pond in 12 ponds at a 45° angle, centred at each pond side and thus facing either to the north, east, south or west. Six of the ponds had a drawdown regime and six a stable water regime. On the 17th of April 2012, 0.5 g seeds were released for each of the 20 plant species (Table 1) in the water of each pond. Although smaller seeded species may have an advantage when colonizing the shore, their ability to germinate upon arrival from fewer resources may be lower. As we do not address this trade-off specifically, we chose to start with equal investment from the parent plants for every species. The use of an equal weight standardizes the species biomass investment in offspring and reflects the trade-off between seed size and seed number (Table 1; Smith & Fretwell 1974; Jakobsson & Eriksson 2000). All seeds were added at once at the lee shore (Southeast side) of the ponds. Within *c.* 45 min, the first seeds had reached the opposite bank/shore and spread evenly throughout the pond. Subsequently, the number of seedlings was counted weekly per section on each mat, and after 8 weeks, the seedlings were identified to species level. None of the seedlings were removed.

SEED BANK EXPERIMENT

For the seed bank experiment, one gradual and one steep mat were placed per pond in an additional set of 12 ponds (6 with stable and 6 with drawdown regime). To create seed banks, 0.5 g seeds of each of the same 20 wetland species as in the dispersal experiment (Table 1) was sown in lines in the soil of these mats and covered with potting soil. Each sowing line ran across the entire length of the mat and received a mixture of two species with distinguishable seedling morphology. The position of the species was randomized among mats. Each week, the number of seedlings was counted per section on the mats, identified to species and removed to avoid competition among seedlings.

DIFFERENCES IN SEED TRAITS BETWEEN SPECIES

For each species, we determined four seed traits related to dispersal (seed floatation capacity and seed weight) and recruitment (Ellenberg F value for soil moisture and seed viability). Seed weight was determined by weighing 40 seeds of each species (in 2 batches of 20, $d = 0.001$ mg). Ellenberg indicators were obtained from the LEDA data base http://statedv.boku.ac.at/zeigerwerte/?#F (Kleyer *et al.* 2008). Floatation capacity of the seeds was determined experimentally by dividing 150 seeds per species equally over five glass jars (diameter of 0.05 m, height 0.11 m), filled with tap water, covered with parafilm to prevent evaporation and stored at room temperature. The number of floating seeds was counted at regular intervals (at $t = 0$, 5, 60 min, 2, 5, 48 h, 1, 2, 3, 4, 5, 6, 7 and 8 weeks) after stirring for 5 s to reduce water surface tension (Danvind & Nilsson 1997). Floatation was calculated per species as their floating half-times, that is, the number of weeks needed for 50% or more of the seeds to sink (T50). If < 50% of the seeds had sunk after 8 weeks, the T50 was set to 8 weeks.

Seed viability was determined by sowing 250 seeds of each species under standard conditions in the glasshouse (21 °C, 16/8 h light–dark regime). One set of standard conditions was chosen to provide an equal opportunity in a similar habitat for all species. For each species, the seeds were divided equally over five plastic pots (diameter of 0.07, height 0.08 m) filled with potting soil (identical as used for the mats). Soil moisture was kept constant at field capacity (0.04 m below soil surface) throughout an 8-week germination period (from 5th May 2012 to 28th June 2012). Germinated seeds were counted and removed weekly.

DATA ANALYSIS

In both the dispersal and seed bank experiment, we analysed the effects of water regime on the number of germinating seeds, the total number of germinated species and the species diversity (Shannon index) after 8 weeks. Comparing the effects of water regime between these experiments yields information on the separate effects of water regime on seed germination conditions and seed dispersal. In the seed bank experiment, we incorporated the effects of shore slope by comparing germination between artificial mats with different angles to the water-table. We tested the effect of water regime on zonation on shore vegetation by analysing the mean elevation of seed germination on the mat for each species and relating this to the species traits Ellenberg value and seed floatation.

STATISTICAL ANALYSES

Data were analysed by multiple generalized linear mixed models (GLMMs) using the package lme4 in ʀ for statistics (R Development Core Team 2013). Normality of residuals and homoscedasticity of variances were verified using Shapiro–Wilk and Levene's tests. Count data were modelled as Poisson distributions with log link function. Significance of terms was determined by likelihood ratio tests (LRT) between models with or without terms of interest. Pearson's product moment correlations were used to detect relations between species traits, the colonized width of the shore and the average elevation of germinating seeds.

Data from the dispersal experiment were analysed in three models (GLMM1–GLMM3). GLMM1 was a repeated measures model over 8 weeks, with the total amount of seedlings per mat per week modelled with Poisson distribution and log link function, depending on the fixed factor Regime, and Bankside and Pond included as random factors (Bankside nested in Pond). In GLMM2, the total number of species per mat was modelled as a Poisson distribution with log link function and in GLMM3 the square-root-transformed Shannon index for the vegetation as a normal distribution. In both models, these dependent variables depended on the fixed factor Regime, with Pond and Bankside as random effects. Bankside was not nested in Pond in the latter two models because this resulted in an equal number of random effects and data points. There were no differences between

banksides when taken as a fixed factor, even though the prevailing wind direction was south-west during the experiment. Bank side was therefore included as a random factor.

Data from the seed bank experiment were also analysed in three GLMMs (GLMM4–GLMM6). Dependent variables were the amount of germinated seeds, as Poisson distribution with log link function (GLMM4); the number of species per mat, as Poisson distribution with log link function (GLMM5); and the square-root-transformed Shannon index for the vegetation, as a normal distribution (GLMM6); depending on Regime, Shore type and their interaction as fixed factors, and Pond included as a random factor in all three models.

Results

DISPERSAL EXPERIMENT

Seeds germinated from all 20 species in the experiment. After 8 weeks, an average of 111 ($\pm$ 38 SE, range 1–682) seedlings was present per species, resulting in a total sum of 2218 seedlings in the dispersal experiment (Table 2). Mats on shores with a drawdown regime, compared with the mats on a stable water regime, retained more seedlings (GLMM1, $\chi^2 = 2839$, d.f. = 1, $P < 0.001$), that is, almost twice as many after 8 weeks (Fig. 1a). On average, the drawdown regime mats harboured almost 50% more species per mat (Fig. 1b, GLMM2, $\chi^2 = 13.1$, d.f. = 1, $P < 0.001$). Together, this resulted in a 20% increase in species diversity (Fig. 1c, GLMM3, $\chi^2 = 8.0$, d.f. = 1, $P < 0.01$).

SEED BANK EXPERIMENT

Seedlings appeared for all 20 species sown on the mats, leading to a total of 73 577 seedlings germinating from the seed bank during 8 weeks (Table 2). The average number of seedlings that germinated per mat during these 8 weeks was higher for the drawdown water regime, but additionally depended on shore morphology (Fig. 2a, Regime $\times$ Shore slope in GLMM4: $\chi^2 = 1612$, d.f. = 1, $P < 0.001$). Under the drawdown regime, the total seedling number was 2.0 times higher on gradual shores compared to steep shores. Shore morphology under the stable regime, however, had no effect on total seedling number.

The number of species per mat was not affected by water-level regime or shore slope (Fig. 2b, Regime $\times$ Shore slope in GLMM5: $\chi^2 = 0.002$, d.f. = 1, $P = 0.96$, after removal of the interaction from the model the single terms Regime and Shore slope still did not significantly affect the number of species per mat: $P > 0.88$). Also the Shannon diversity of the seedling community was not significantly affected by water-level regime or shore slope (Fig. 2c, Regime $\times$ Shore slope in GLMM6: $\chi^2 = 1.9$, d.f. = 1, $P = 0.16$). After removal of this interaction, diversity tended to be slightly, but not significantly, higher at the steep shores ($\chi^2 = 3.6$, d.f. = 1, $P = 0.06$), but absolute differences were very small (Fig. 2c). Water-level regime did, after removal of the interaction, still not affect species diversity ($\chi^2 = 1.0$, d.f. = 1, $P = 0.32$).

SPECIES TRAITS

Floatation capacity, Ellenberg moisture preference and seed weight were not correlated with each other for this set of species (Table 3). Seed viability, measured as percentage germination under field capacity conditions in the glasshouse, differed considerably between the species sown in equal amounts under standard conditions. This variation could not be related to seed floatation capacity or weight; however, seed

Table 2. Seed characteristics of the 20 plant species studied
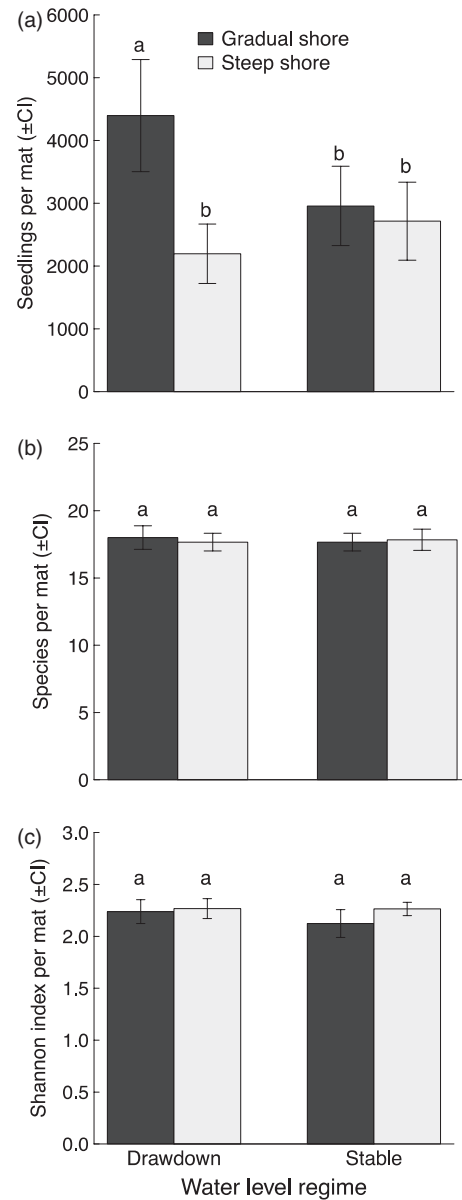
Species	Floatation duration	Seed viability	Dispersal number	Seed bank number
Alisma plantago-aquatica	1 ± 0	0.0 ± 0.0	10	264
Butomus umbellatus	6.1 ± 1.6	0.0 ± 0.0	11	95
Calla palustris	8 ± 0	36.0 ± 11.9	41	453
Caltha palustris	1.2 ± 1	28.0 ± 9.4	47	1598
Carex pseudocyperus	4.7 ± 1.3	4.0 ± 2.8	148	581
Carex vulpina	1.1 ± 0.6	0.0 ± 0.0	1	13
Eupatorium cannabinum	0.7 ± 1.6	44.0 ± 11.5	44	3672
Filipendula ulmaria	1.8 ± 1.1	59.2 ± 12	137	2321
Glyceria maxima	4.9 ± 1.1	40.8 ± 14.5	14	1422
Hierochloe odorata	5.7 ± 1.5	12.8 ± 7.8	10	824
Holcus lanatus	7.3 ± 0.4	94.8 ± 3	209	8798
Hypericum perforatum	2.5 ± 1.4	79.6 ± 8.3	18	5838
Lychnis flos-cuculi	1.9 ± 3.1	57.2 ± 2.7	409	5118
Lycopus europaeus	8 ± 0	49.2 ± 18.4	18	2624
Lythrum salicaria	6.8 ± 1	52 ± 12.5	262	18 313
Mentha aquatica	8 ± 0	66.8 ± 10.7	682	8125
Rumex hydrolapathum	8 ± 0	34.8 ± 12.2	55	438
Stachys palustris	4.2 ± 3.3	15.6 ± 7.9	11	194
Urtica dioica	5.5 ± 1.9	85.2 ± 6.1	35	1756
Veronica beccabunga	1.4 ± 1.1	89.6 ± 2.0	56	11 130

Data presented are floatation capacity, defined as number of weeks required for 50% of seeds to sink within containers [mean $\pm$ standard deviation (SD)], seed viability, expressed as percentage of germinating seeds (mean $\pm$ SD, $n = 5$), dispersal number (total number of seeds that germinated in the dispersal experiment) and seed bank number (total number of seeds that germinated in the seed bank experiment).
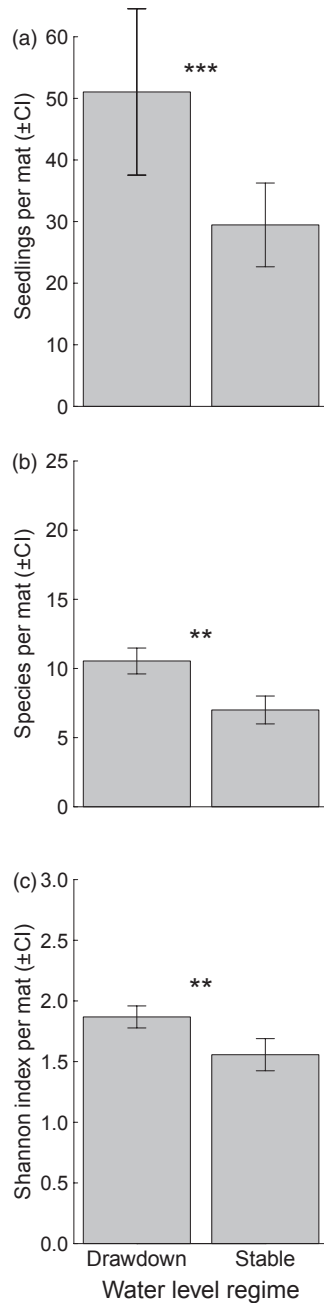
Fig. 1. Effect of drawdown and stable water-level regimes in the dispersal experiment on (a) the number of seedlings, (b) species richness and (c) diversity of the seedling community. Data are mean per mat after 8 weeks; vertical bars indicate $\pm$ 95% CI. Significance level from GLMMs are **$P < 0.01$, ***$P < 0.001$.

Fig. 2. Effect of water-level regime and shore slope in the seed bank experiment on (a) number of seedlings, (b) species richness and (c) diversity of the seedling community. Data are mean number of seeds that germinated over 8 weeks per mat; vertical bars indicate $\pm$ 95% CI. Means that do not share a common letter differ significantly at $\alpha = 0.05$.

viability decreased with increasing Ellenberg value (Table 3). In the dispersal experiment under the drawdown regime, seed floatation capacity did not affect the average elevation where seeds germinated on the shoreline, but positively correlated with the width of the shore that species colonized (Table 4). On the gradual slopes of the seed bank experiment, there was a trend in the data towards species with a higher Ellenberg value germinating better on a lower elevation on the mats during the drawdown regime (Table 4). However, this

relationship was not significant and not seen on the steep slopes, and there were no correlations between moisture preferences and the elevation or width of species on the shore for either slope type.

Discussion

Seed establishment on the shore was found to be affected by interactions between water levels, shore morphology and species traits. Our experiments show how water levels affect seed dispersal and germination, and therewith provide added mechanistic explanations for observed effects of fluctuating water

Table 3. Pearson's product moment correlations among species traits for wetland plant species (see Tables 1 and 2 for the values per plant species)

	Seed weight	Ellenberg value	Floatation T50
Seed viability	$r = -0.21$, $P = 0.37$	**$r = -0.50$, $P = 0.024$**	$r = 0.12$, $P = 0.61$
Floatation T50	$r = 0.38$, $P = 0.097$	$r = 0.16$, $P = 0.50$	
Ellenberg value	$r = 0.30$, $P = 0.20$		

Variables are seed weight in mg, Ellenberg value for soil moisture, seed floating half-times in weeks as determined in the floatation experiment and seed viability as percentage germination determined under field capacity in the glasshouse. Significant values at the $\alpha = 0.05$ level are in bold.

Table 4. Pearson's product moment correlations of the species traits floatation capacity (floating half-times, T50) and soil moisture preference (Ellenberg value), with the mean elevation at which species germinated on the mat (mean elevation) and the total width they colonized on the mats (total width)

		Mean elevation		Total width	
Experiment	Shore	r	P	r	P
Floatation	Dispersal	0.41	0.56	**0.50**	**0.025**
Ellenberg	Dispersal	−0.31	0.19	0.17	0.46
Ellenberg	Seed bank	Steep	−0.35	0.13	−0.25	0.27
Ellenberg	Seed bank	Gradual	−0.42	0.06	−0.20	0.41

Correlation r-values and corresponding P-values are indicated for the two experiments under the drawdown regime treatment ($n = 20$). Significant values at the $\alpha = 0.05$ level are in bold.

levels on the ultimate plant community composition in the field on much larger spatial scales (Jansson *et al.* 2005; Nilsson *et al.* 2010; Raulings *et al.* 2010, 2011; Greet, Angus Webb & Cousens 2011). Fluctuating water levels enhanced germination from the soil seed bank on the gradual shore as well as settlement of seeds dispersed by hydrochory. Seed floatation ability was an important species trait enhancing dispersal, and affected how species profited from water-level fluctuations.

COMMUNITY ZONATION AND INTERSPECIFIC TRAIT
DIFFERENCES

Wetland plant communities often show a typical zonation, where species form lateral bands corresponding to the elevation of the shore and distance from the edge of the water (Grace & Wetzel 1981; Coops & van der Velde 1995; Lenssen, ten Dolle & Blom 1998; Engels, Rink & Jensen 2011). This zonation is often found on the shores of ponds and lakes, but it can also be found on lentic sections of rivers, both in temperate and other regions of the world (Casanova & Brock 2000; Parolin 2001). Various hypotheses exist to explain shore vegetation zonation. Zonation can be caused by

a difference between species in their ability to cope with inundation, leading to species-specific survival and therefore zonation (Coops, van den Brink & van der Velde 1996; Lenssen, ten Dolle & Blom 1998). It may also already occur during the seed and seedling phase, which are generally considered as the most critical life stages of a plant (Schupp 1995; Weiher & Keddy 1995; Parolin 2001). Experimental work in a flume-tank set-up has, for instance, shown that seeds will be systematically delivered to particular sections of the shore (Merritt & Wohl 2002). If seeds with different characteristics are stranding repeatedly to different sections of the shore, or differ in moisture preferences for germination, these processes may already cause zonation during initial community assembly, or even before the start of germination.

In our dispersal experiment, we tested whether interspecific differences in seed floatation would affect the dispersal of seeds potentially resulting in vegetation zonation on freshwater shores. Directed dispersal like this has previously been shown for woody riparian species, whereby seeds were found to be deposited at sections of the shore with particular gravel size and location to the height of the surface water-table (McBride & Strahan 1984). For floodplain species, the time of seed release has been shown to be related to timing of water discharge in rivers, such that lower sections of the shore would be colonized (Menges & Waller 1983). Other species may form aerial seed banks instead of relying on the soil seed bank, and those do not regulate their seed release in response to surface water levels but respond to other environmental triggers (Hamilton-Brown *et al.* 2009). Nevertheless, also for these species, surface water levels may be important as this affects secondary seed dispersal, the moisture conditions on the seed deposition site, and hence germination and seedling establishment success. These studies all suggest that processes in the seed and seedling phases can create zonation, as well as influence the height distribution of seeds in the soil seed bank (O'Donnell, Fryirs & Leishman 2013).

We here found that the floating capacity of seeds was an important factor enhancing the colonization of new sections of the shoreline, as it increased the likelihood of seeds stranding on the shore. Especially plants with high seed floatation capacity profited from the gradual lowering of the water level, because this facilitated deposition of seeds on a wider section of the shore. However, there was no relationship between mean elevation on the shore where species established and seed floatation, and therefore no indication of zonation through this mechanism.

These results of our seed dispersal and soil seed bank study may apply to clonal forms of regeneration as well, although their dependency on seeds may differ. Wetland plants frequently disperse by fragments that also vary in their floating capacity (Grace 1993; Sarneel 2013). However, the interactive effects of surface water-table dynamics and plant fragment traits on their dispersal and establishment should be further investigated.

Besides seed floatation capacity, the soil moisture preference of seeds for germination was hypothesized to determine where species germinate, which may also lead to zonation

already during the seedling stage. Glasshouse experiments show that different species can prefer different moisture conditions for germination (Coops, van den Brink & van der Velde 1996; Nygaard & Ejrnaes 2009; Geissler & Gzik 2010), proposing that interspecific differences in seed germination can also strongly contribute to zonation. In our outdoor experiments, there was only a trend towards a negative relationship between Ellenberg moisture value and mean elevation of seed germination at the gradual slope of the seed bank experiment. As this relation was not significant and only present on the gradual slope, we have no conclusive evidence that Ellenberg values are a major explanatory factor for community zonation of wetland plants in the seedling stage. As a result, the alternative hypothesis that all species germinate equally well once sufficient moisture is provided to germinate is best supported by our data. Water regime and shore morphology were stronger determinants for shoreline plant diversity.

The lack of strong species-specific responses to water-level treatment in our experiments is in line with previous studies that also did not observe a species-specific germination response to water level (Lenssen, ten Dolle & Blom 1998; Boedeltje, ter Heerdt & Bakker 2002), but contrasts with studies that found a relationship between Ellenberg moisture values and germination conditions (Coops, van den Brink & van der Velde 1996; Nygaard & Ejrnaes 2009; Geissler & Gzik 2010). An explanation for these contradictory results among studies could be the selection of plant species tested and the range of Ellenberg values that was included in the experiments (in our experiment: Ellenberg 4–10). As indicated in Table 1, life-history strategies between the plants differed only slightly, which indicates that our findings are representative for perennial hemicryptophytes. Possibly, soil moisture preferences become more relevant when including species that prefer more extreme conditions, for example with adaptations to germinate at complete waterlogged (Ellenberg value 12) conditions.

The lack of evidence for strong zonation at the seedling stage in our experiments suggests zonation of wetland plant communities may more likely be the result of processes at a later developmental stage, for instance, due to interspecific competition for light or nutrients (Coops & van der Velde 1995; Kotowski *et al.* 2006, 2010; Engels, Rink & Jensen 2011). As our experiment was focused on the initial community assembly from dispersed and soil seed bank seeds and therefore lasted 8 weeks, we cannot draw conclusions about the role of competition during later life stages or with already established vegetation. We can conclude from our experiments that we did not find evidence for zonation at the initial seedling establishment phase.

COMMUNITY DIVERSITY

The current decline of plant species richness in north-west Europe can, among other factors, significantly be attributed to a loss of seed dispersal capacity, especially for hydrochorously dispersed seeds (Ozinga *et al.* 2009; Brederveld *et al.* 2011). Whereas flow regime and discharge importantly deter-

mine seed deposition patterns in faster-flowing river systems (Merritt & Wohl 2002), water regulations in ponds and lentic parts of rivers are similarly influenced by water-level fluctuations. We here hypothesized that if stabilization of the water levels caused the observed species declines, our experimental drawdown regime would positively affect seed dispersal and germination compared to a stable regime. Indeed, the number of germinating seedlings was positively affected by drawdown, in both the dispersal and seed bank experiment. Interestingly, species number and diversity were only affected by the water fluctuations in the dispersal experiment. While the Shannon diversity index in the seed bank experiment was very close to the Shannon index of the added seed mixture (2.47 or 2.09, without and with correction for seed viability, respectively), it was much lower on the banks in the dispersal experiment. This indicates that dispersal exerted strong species sorting in this experiment, that is, not all seeds reached the mats. When not all species are already present (for instance, in the soil seed bank), a drawdown water regime can have a strong positive effect on the establishment and diversity of hydrochorously dispersing species.

In comparison with seasonal fluctuations in water levels with low amplitude, of which we here show positive effects on community diversity, long-term flooding events with another seasonal timing or with larger amplitude and durations may affect seed dispersal and germination differently (Casanova & Brock 2000; Nygaard & Ejrnaes 2009; Raulings *et al.* 2011). Flooding may prohibit germination directly (Salter *et al.* 2010b), and prolonged flooding can even eliminate species that are not resistant to the low oxygen levels, toxicity or important changes to soil chemistry generally associated with flooding (Kotowski *et al.* 2010; Salter *et al.* 2010a; Unger, Muzika & Motavalli 2010). Given the low germination of seeds in our experiments below the water line under a stable regime, prolonged flooding may therefore not promote community diversity as positively as the short-term drawdown fluctuation in our experiments. Overall, short-term flooding events or a gradual natural drawdown water regime on the time-scale of weeks in spring and early summer can increase seed dispersal and deposition, and can therewith increase community diversity. We find this experimentally in a temperate region of the world, but we expect similar springtime processes to occur in other regions of the world.

INTERACTIVE EFFECT OF SHORE MORPHOLOGY AND WATER-LEVEL REGIME ON SEED BANK GERMINATION

The drawdown water regime increased the germination of soil seed bank seeds at gradual shores, however, not at steep shores. This may have been due to the enlargement of zones with moist, but not flooded, conditions at the drawdown regime, which may increase total seed germination. This corresponds to glasshouse experiments that indicate that most wetland species germinate at moist soil conditions (Boedeltje, ter Heerdt & Bakker 2002). Consistent with the fact that the drawdown zone was twice as large at the gradual shore

slope than at the steep slope, two times as many seedlings germinated at the gradual shore. This suggests that water regime and shore morphology merely affected the space available for germination rather than germination itself. The availability of shore habitat can be a restricting factor for establishing vegetation, as was also observed in rivers (Andersson, Nilsson & Johansson 2000). Our mesocosm study thus suggests that at small spatial and short temporal scales, a gradual shore slope can positively affect soil germination conditions. However, on a large scale, wetlands often have complex topographical structures, whereby a drawdown regime can increase germination in some parts while decreasing germination in other parts. Whether or not the overall effect of a drawdown regime is positive or not, therefore depends largely on the wetland topography, spatial scale and timing of water fluctuations (Raulings *et al.* 2011). Our study nevertheless shows that upon restoration of natural wetland vegetation, among the many factors that should be addressed (Bakker *et al.* 2013), also shore morphology and water-level fluctuations are important processes to consider.

Conclusion and implications

Fluctuating water levels affect seed dispersal and germination from the soil seed bank on the shore. A drawdown water regime affects the establishing seedling community most during the dispersal phase, as it enhances seed deposition and creates more space with suitable germination conditions. Species traits were moderators of these effects, as seed floatation capacity determined the width of the zone over which deposition occurred, but species moisture preferences played hardly a role. This nevertheless indicates that wetland plant communities are already influenced by water levels during the germination phase, which is important for our fundamental understanding of how wetland plant communities develop and has implications for wetlands with active water level and shore management.

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository (van Leeuwen *et al.* 2014). Dispersal Jrl Ecol 2014.xlsx contains all the weekly seedling counts for the mats in the seed dispersal experiment. Seed bank Jrl Ecol 2014.xlsx contains all the seedling counts over time for the seed bank experiment.

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