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Local flooding history affects plant recruitment in riparian zones

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Abstract

Aims: Many rivers across the globe are severely impacted by changed flooding regimes, resulting in drastic shifts in vegetation, but the processes driving the exchange of flood-sensitive and flood-tolerant species are understood less. We studied the role of long-term and recent flooding histories for riparian plant recruitment in response to various changes in flooding regime.

Location: Vindel River catchment (Northern Sweden).

Methods: We experimentally changed long-term flooding regimes by transplanting turfs between high and low elevations in 2000 and in 2014 (*n* = 8 per treatment). We sowed seeds of five riparian species in both transplanted turfs and non-transplanted controls and counted seedling numbers over two growing seasons. Further, we inventoried natural seedling frequencies in 190 plots in 19 reaches in 2013 and 2014, and related natural seedling numbers to plot flooding history in the period 2012–2014.

Results: We observed effects of long-term flooding history in the second year of the transplantation study (2015), but not in the first year. In 2015, turfs transplanted to locations with less flooding resulted in higher plant recruitment while transplantation to sites with more frequent flooding reduced recruitment compared to the controls. Since these differences were only found in recently transplanted turfs and not in older turfs, the legacy effect of long-term flooding history can be transient. In the field seedling survey, similar differences were found between flooding-history categories in 2013, but not in 2014, when the moisture conditions of the most recent year determined flooding. Further, lowest seedling numbers were observed when the previous flooding occurred in winter, and higher seedling numbers when floods occurred in spring or not at all.

Conclusions: Both long-term and recent flooding histories can affect plant recruitment, and their influence should be taken into account when designing restoration projects.

KEYWORDS
dispersal filtering, environmental filtering, flood dynamics, historic contingency, legacy effects, plant recruitment window, regime shifts, window of opportunity, zonation

1 | INTRODUCTION

Plant communities are dynamic, subjected to continuous change due to species interactions, colonisation and extinction, aided by stochastic or predictable disturbances (Li & Pennings, 2016; Mahoney & Rood, 1998; Menge & Sutherland, 1987; Pennings & Callaway, 1992). The interface between water and land along rivers and streams (riparian ecosystem) is one of these very dynamic and frequently disturbed ecosystems, and due to its important ecosystem services (Naiman & Décamps, 1997), understanding what shapes these species-rich plant communities has become critical. Such knowledge is also increasingly important since almost all river systems worldwide are threatened by flow management and climate change that can drastically alter the flow regime (Hirabayashi et al., 2013; Nilsson, Reidy, Dynesius, & Revenga, 2005; Winemiller et al., 2016). Extreme flooding events, but also years with extreme droughts are predicted to become more common (Hirabayashi et al., 2013). Because of the direct consequences of the flooding regime for dispersal, germination, establishment, and growing conditions, such changed flooding regimes can induce vegetation changes. However, we have limited insight in how processes such as germination and establishment lead to these changes (Beauchamp & Stromberg, 2007; Fraaije, ter Braak, Verduyn, Verhoeven, & Soons, 2015; Levine & Stromberg, 2001; Nilsson, Jansson, & Zinko, 1997; Ström, Jansson, Nilsson, Johansson, & Xiong, 2011).

Species exhibit a range of traits to cope with flooding events (Bornette & Puijalon, 2011), and interspecific differences create an elevational zonation in riparian zones. At low elevations, plant communities that are adapted to frequent flooding dominate while species that are less tolerant prevail at higher elevations (van Eck, van de Steeg, Blom, & de Kroon, 2004). We know from greenhouse studies that flooding for a few days to a week is sufficient to kill mal-adapted species (Garssen, Baattrup-Pedersen, Voesenek, Verhoeven, & Soons, 2015; van Eck, Lenssen, van de Steeg, Blom, & de Kroon, 2006). In the field, however, changes in vegetation community composition after changed flow regimes mostly occur slowly (Hasselquist et al., 2015; Sarneel et al., 2019; Ström et al., 2011; van Eck et al., 2004), indicating that other processes may interact.

In order to replace the mal-adapted species, the better-adapted species will have to arrive, germinate and establish under the new conditions, and these processes take time. Separate studies have confirmed the link between flow regime and dispersal (Bourgeois, Gonzalez, Vanasse, Aubin, & Poulin, 2016; Fraaije et al., 2015; Soomers et al., 2011) and with habitat characteristics important for germination and establishment, such as soil moisture (Kotowski, Beauchard, Opdekamp, Meire, & van Diggelen, 2010; Luo et al., 2016; Sarneel, Janssen, Rip, Bender, & Bakker, 2014) or sedimentation (Levine & Stromberg, 2001). Since germination and early establishment are hard to separate under field conditions, they are collectively referred to as recruitment in this study.

Next to the direct effects of changed flooding regimes, however, there are indications that historic factors may influence a range of processes, including recruitment (Fukami, 2015; Sarneel, Kardol, &

Nilsson, 2016). As a consequence, specific events or other past environmental conditions can have long-lasting effects on vegetation composition (Sarneel et al., 2019). For example, the few available tree ring studies show that almost all trees established directly after flow stabilization events (Beauchamp & Stromberg, 2007; Braatne, Jamieson, Gill, & Rood, 2007; Greene & Knox, 2014), and differences in timing of the flood pulse can drastically change patterns in seedling abundance between years (Dixon, 2003).

These studies indicate that flooding history could affect seedling recruitment in several ways. First, in situations where long-term flooding regimes change (e.g., after regulation, restoration or through climate change), past conditions may still govern many of the processes after the regime change, via so-called legacy effects. Next to that, a recent history of specific flooding events can have large consequences, e.g., through direct effects on plant mortality or the supply of seeds. Last, recent flooding history will determine if the post-flood period is long enough for seedlings to grow sufficiently large to survive the next flood. Flooding history can thus play a role via legacy effects of long-term flooding regimes and more recent flooding events, and by determining the so-called disturbance-free 'window of opportunity for germination' or 'recruitment window' (Balke, Herman, & Bouma, 2014; Mahoney & Rood, 1998; Rankin & Pickett, 1989).

To study these roles of flooding history we set up a turf transplantation experiment, where we followed the recruitment of sowed seeds in turfs that were transplanted between flooding regimes and inventoried natural seedling distributions in riparian zones with contrasting histories of flooding events. We hypothesised that (a) if legacy effects of long-term flooding regimes are important, recruitment would be different in transplanted and non-transplanted control turfs. Depending on how long such legacy effects may persist, we would observe this difference not only in turfs transplanted one year ago, but also in turfs transplanted more than one decade ago. In our seedling survey of natural plots, we hypothesised (b) that there will be a difference in number of seedlings in plots with a different recent flooding history. Because longer disturbance-free periods may increase seedling survival (Mahoney & Rood, 1998), we hypothesized that (c) longer recruitment windows may correlate positively with number of natural seedlings.

Deepened insight in the role of long-term and recent flooding history may be especially important in boreal zones, where climate change effects are predicted to be larger than in other parts of the world, inducing drastic changes in timing and likely also in magnitude of the flood pulse due to the change in precipitation from snow to rain (Nilsson, Riis, Sarneel, & Svavarsdottir, 2018).

2 | MATERIALS AND METHODS

We tested the effects of flooding history (a) after experimentally induced changes in flood regime in a 2-year soil transplantation experiment and (b) for natural seedling densities along the riparian zones of the Vindel River and its tributaries in a seedling survey.
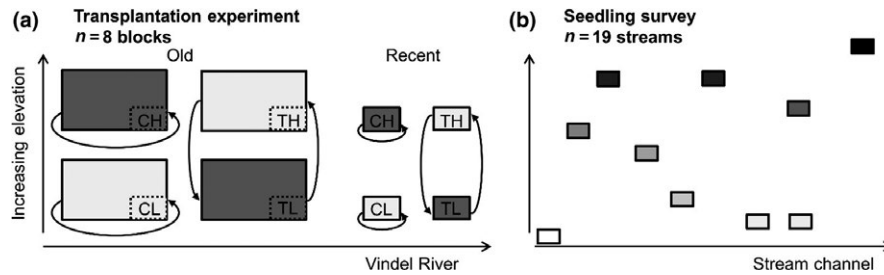
FIGURE 1 Experimental setup: Schematic overview of (a) transplantation experiment and (b) seedling survey. Lighter colours indicate plots (a) transplanted from and (b) located at lower elevations. CH; control at high elevation, CL; control at low elevation, TH; transplantation to high elevation, TL; transplantation to low elevation, for turfs transplanted in 2000 (old) and 2014 (recent). Arrows indicate the direction of transplantation. Subplots for sowing are indicated with dashed squares in the old turfs, which are larger as the remaining area is used for long-term vegetation surveys (Sarneel et al., 2019; Ström et al., 2011). Transect length in b was 100 m. Due to the variable width of the riparian zone, the vertical distribution of the plots was determined as the percentage of the riparian width

2.1 | Study area

The Vindel River (64°49′ N, 18°51′ E) has a mean annual discharge of 188 m³/s at the point where it joins the Ume River (2000–2015, Swedish Meteorological and Hydrological Institute, SMHI), and has a boreal climate. Flow regimes in the Vindel River catchment are characterised by spring floods in May or June, with the flood peak and duration depending on the amount of snow, spring temperatures, and how much the soil permeability is affected by frost. In smaller tributaries, floods during autumn and winter can occur due to rain events and ice jams, respectively. The soil transplantation experiment was located in a floodplain along the main stem of the Vindel River, 100 km from the mouth and near the village of Strycksele. The riparian vegetation there is characterised by graminoids at the lowest elevation, willow shrubs at intermediate elevations, forbs and grasses at the highest elevation and mixed birch and pine forest bordering terrestrial ecosystems (Sarneel et al., 2019; Ström et al., 2011).

The inventoried tributaries in the seedling survey were all restored from timber-floating structures in a basic or a more enhanced way. At the time of this study, the two different restoration types had no measurable effect on most ecological parameters, including plant cover, soil moisture and germination (Herberg & Sarneel, 2017; Nilsson et al., 2017), and we therefore did not consider restoration type in our analysis.

2.2 | Transplantation experiment of long-term flooding history

In 2000 and 2014 we excavated soil turfs along the river bank in Strycksele, using eight replicated random blocks spread over a ca. 250 m long reach, which was 15 m–35 m wide. Each block consisted of eight turfs (Figure 1), with four turfs at low elevation (in the tall-graminoid zone) and four turfs at high elevation (species-rich grassland). The turfs at low and high elevation differed on average 1.86 m (± 0.06 SE) in elevation. Within each block, two turfs (70 cm × 100 cm) at high and two at low elevations were excavated in June 2000 (referred to as "old turfs"). The other four turfs (20 cm × 30 cm) in each block were excavated shortly after soil thawing and before the spring flood in May 2014 (referred to as "recent turfs"). Turfs included whole

plants and were excavated to ca. 20 cm depth, deeper than the rooting zone. The turf size in 2000 was larger than in 2014 because Ström et al. (2011) and Sarneel et al. (2019) used the old turfs for vegetation monitoring. To be able to compare recent and old turfs we only used a 20 cm × 30 cm area in a corner of the old turfs (Figure 1).

In both 2000 and 2014, half of the excavated turfs on both high and low elevations were rotated 180° and carefully put back in the same location as a control (Figure 1a). The other turfs were placed in cradles and transplanted to their new elevations. Controls at high (CH) and low (CL) elevation experienced a normal flooding regime while the transplanted turfs at high elevation (TH) have low-elevation flooding history (yearly flooding) and the transplanted turfs at low elevation (TL) have a high-elevation history of infrequent short floods (Figure 1a). Each treatment block included a recent and an old turf of each transplantation treatment, which allowed testing for legacy effects of long-term flooding history, and to see if such legacy effects can persist.

Plots along free-flowing rivers like the Vindel River likely receive a seed mixture of terrestrial, wetland and aquatic species (Bourgeois, Boutin, Vanasse, & Poulin, 2017; Goodson, Gurnell, Angold, & Morrissey, 2001; Merritt, Nilsson, & Jansson, 2010). In each turf, we sowed seeds of *Betula pubescens*, *Solidago virgaurea*, *Achillea millefolium*, *Rumex acetosa* and *Carex acuta* to represent the riparian community (Table 1). Thirty seeds per species were sown in one 10-cm-long line directly after the spring flood 2014, as this is a natural arrival time for seeds in the system. Sowing overcomes dispersal limitations and allows us to study the effects of flooding history on recruitment. Seedling numbers were counted per species on 19 September 2014 and 22 July 2015. The relative change in seedling abundance between 2014 and 2015 was calculated as ([seedlings 2015 – seedlings 2014] / [seedlings in 2014]) * 100. When seedling numbers were 0 in 2014 and increased in 2015, which would result in dividing by zero, we defined the relative change in seedling abundance as 100. In July 2015, the aboveground biomass of the seedlings was harvested, and dried at 60°C for 72 hr before being weighed. Average seedling biomass was calculated by dividing total seedling dry weight by the total number of seedlings per turf.

To provide background habitat characteristics of the turfs we measured soil pH in May 2014, by shaking 5 g soil with 50 ml

TABLE 1 Species characteristics

Species	Original elevational position	Ellenberg F-value	Viability (%)
Betula pubescens Ehrh.[a]	High	3.75	12
Solidago virgaurea L.[b]	High	3.75	69
Achillea millefolium L.[c]	High	5.25	96
Rumex acetosa L.[c]	Intermediate	5.5	93
Carex acuta L.[b]	Low	5.5	3

Typical elevation. Ellenberg moisture preference indicator value for the species' fully developed adult individuals (Synbiosis database; Hennekens, Smits, & Schraminée, 2010), with 1 being very dry and 12 submerged. The average number of seeds sown per turf, and the experimentally determined viability of the sown seeds as the germination percentage of 100 sown seeds ($n = 5$) in the greenhouse under 20°C.

Seeds obtained from [a]Svenska skogsplantor, Hallsberg, Sweden, [b]Jelitto Staudensamen GmbH, Schwarmstedt, Germany, [c]Cruydt-Hoeck, Nijeberkoop, the Netherlands.

demineralized water for 4 hr. In August 2014 we took another soil sample and determined C and N contents (% of dry weight) with a FLASH 2000 Organic Elemental Analyser (Interscience, Breda, The Netherlands). Turf elevation was measured using a total station (Trimble S8 DR-Plus; Trimble, Sunnyvale, CA, USA). Total vegetation cover was estimated visually, rounding to the nearest 10%. Flood duration for high and low turfs was calculated using discharge data obtained from SMHI (vattenwebb.smhi.se).

2.3 | Seedling survey and recent flooding history

To study if recent flooding history and specific flooding events affect seedling densities in the field, we inventoried natural seedling communities in tributaries throughout the Vindel River catchment in August 2013 and 2014. In 19 reaches with a length of 100 m, the number of seedlings was counted in ten 50 cm × 100 cm large plots, placed with 10-m intervals at different distances perpendicular from the main channel. Plots were distributed following the same scheme in each reach between the summer low and spring high-water levels (Figure 1b). In each plot, we counted the number of seedlings (<3 cm tall plants). Water-level fluctuations were measured with a 4-hr interval using pressure divers (In-Situ Inc, Ft. Collins, CO, USA) and a barometer pressure logger that also recorded temperature, between October 2011 and September 2014. Plot elevation was measured as the vertical distance from the middle of the plot to water level at the time of measuring to enable calculation of flooding parameters per plot.

2.4 | Calculations and statistics

In the turf transplantation experiment, effect of treatment (four levels; CH, CL, TH, TL) and turf age (recent vs. old) on seedling numbers in 2014 and 2015 were analysed using a generalized linear mixed model (GLMM) with a Poisson distribution and random effect of treatment block. We analysed total seedling numbers since the selected species were common species and seedling counts per species were too low to give meaningful results. For the relative change in seedling abundance (supplementary material S1) and seedling biomass, we used linear mixed models (LMM)

with a Gaussian distribution. Comparisons between the model with and without the parameter of interest were used to determine the significance of the fixed-factors treatment and experimental duration (Crawley, 2007). Interactions with a p-value < 0.05 were evaluated with a Tukey post-hoc test using the lsmeans package in R (Lenth, 2016).

For the natural seedling survey in the 19 reaches, we calculated when a plot was flooded, with a flooding event defined as a water level above the middle of the plot for at least five or more consecutive days, as such flooding duration starts to be detrimental for seedlings of flood-sensitive species. We classified the plots in four flooding history classes, which resemble the treatments in the transplantation experiment: (a) DF: 'increased flooding', absolute flooding duration of the plot doubled compared to the previous year; (b) FD: 'increased drought' absolute flood duration decreased with 50% compared to the previous year; (c) DD: 'drought' not flooded but dry for two consecutive years; and (d) FF: 'flooded', flooded yearly. Differences in seedling numbers and species richness of the vegetation were tested in R 3.4.3 as before, with GLMM assuming a Poisson distribution and LMM, respectively.

From the water level fluctuations, we also calculated the number of days that had passed since the last flooding event (of five days or longer), with a maximum of 750 in 2013 and 1,066 in 2014, which was the number of days that we logged the water level. Time since last flood was log + 1-transformed and correlated to the number of seedlings per plot using Pearson correlations in R 3.4.3.

3 | RESULTS

3.1 | Environmental conditions in the transplantation experiment

In August 2014, turfs at high elevation had drier, slightly more acidic soils than those at low elevation (Table 2), but this difference in pH was not significant. Total soil carbon and nitrogen concentrations did not differ between elevations in August 2014 (Table 2). In 2014, turf vegetation cover was close to 100% for all old turfs and the recent turfs at high elevation (CH and TH). At low elevation, the cover

TABLE 2 Differences in site characteristics at high and low elevation (±SE) tested with a paired *t*-test

Variable	N	High	SE	Low	SE	p
Flooding duration 2015 (days)	32	0		25.7	0.24	
Soil moisture (% weight, Aug.)	8	24.5	1.15	36.3	1.54	<0.001
Soil pH	8	5.48	0.07	5.71	0.07	0.066
Soil total N (%)	8	0.29	0.04	0.31	0.04	0.597
Soil total C (%)	8	4.11	0.50	4.77	0.57	0.388
Vegetation cover 2014, recent	8	80.0	28.3	9.10	3.22	
Vegetation cover 2014, old	8	92.5	32.7	88.8	31.4	
Vegetation cover 2015, recent	8	90.6	32.0	8.20	2.87	
Vegetation cover 2015, old	8	58.8	20.8	26.9	9.50	

Vegetation cover is that of the turfs transplanted between elevations.

TABLE 3 Statistical results of the GLMM and LMM testing treatment and turf age on seedling numbers, relative change in seedling abundance, and biomass

	Year	Treatment			Turf age			Treatment ×Turf age		
		df	χ^2	p	df	χ^2	p	df	χ^2	p
Seedlings	2014	3	83.13	<0.001	1	135.32	<0.001	3	8.92	0.030
Seedlings	2015	3	233.28	<0.001	1	256.34	<0.001	3	10.75	0.013
Abundance change		3	21.79	<0.001	1	7.37	0.007	3	8.15	0.043
Biomass	2015	3	0.68	0.877	1	0.42	0.518	2	1.81	0.404

Treatment accounts for the different turf transplantation treatments (control at high elevation, control at low elevation and transplanted to high or low elevation) representing differing flooding histories. Turf age accounts for the differences between recent and old turfs.

was intermediate in recent CL turfs and lowest in the recent TL turfs. Differences between treatments were about the same in 2015, although absolute covers in the old turfs were somewhat lower than in 2014 (Table 2).

3.2 | Recruitment in the transplantation experiment

All sown species germinated and we counted on average 16.1 (± 2.15 SE) and 5.6 (± 1.53 SE) seedlings per turf in 2014 and 2015, respectively. *Rumex*, *Achillea* and *Solidago* were found in most of the turfs in both years, while *Betula* and *Carex* germinated poorly. We observed only very few seedlings of non-experimental species in 2014 and none in 2015. In both 2014 and 2015, we found a significant interaction between transplantation treatment and turf age (Table 3), but the post-hoc test showed very different patterns in recruitment in both years (Figure 2).

In 2014, we observed more seedlings at low elevation in both recent and old turfs (Figure 2a). In addition, there was a trend towards more seedlings in recent turfs, except that in the controls at high elevation (CH), only few seedlings were found in both recent and old turfs. Conversely, in 2015, more seedlings were found at high elevation than at low elevation, and strikingly different seedling numbers were found in transplanted turfs that had different flooding histories compared to the control (Figure 2b). That is, we found enhanced

recruitment in the TH treatment (decreased flooding) compared to the controls (CL and CH), while in the TL treatment (increased flooding), less seedlings were found compared to both controls (CL and CH). In old turfs, installed in 2000, absolute seedling numbers were low and differences between treatments small. Patterns in old turfs merely reflected the overall difference between high and low elevations that we also observed in the recent turfs in both 2014 and 2015. In line with the big changes in seedling numbers at high and low elevations, relative seedling abundance increased at high elevation compared to low elevation, especially in recent turfs (Figure 2c). Even though the mean seedling number decreased over the study period in recent turfs with CH treatment, the relative seedling abundance increased, which was due to it being expressed as a ratio. Average biomass per seedling was not significantly affected by transplantation treatment nor by turf age (Figure 2d). Patterns of the individual species reflected the general pattern rather well, especially in 2015 (Appendix S1).

3.3 | Environmental conditions in the seedling survey

Large differences in magnitude and flooding frequency were observed between the sampled reaches and years, with a somewhat larger peak flood in 2012 compared to the other years (Figure 3). More than half of
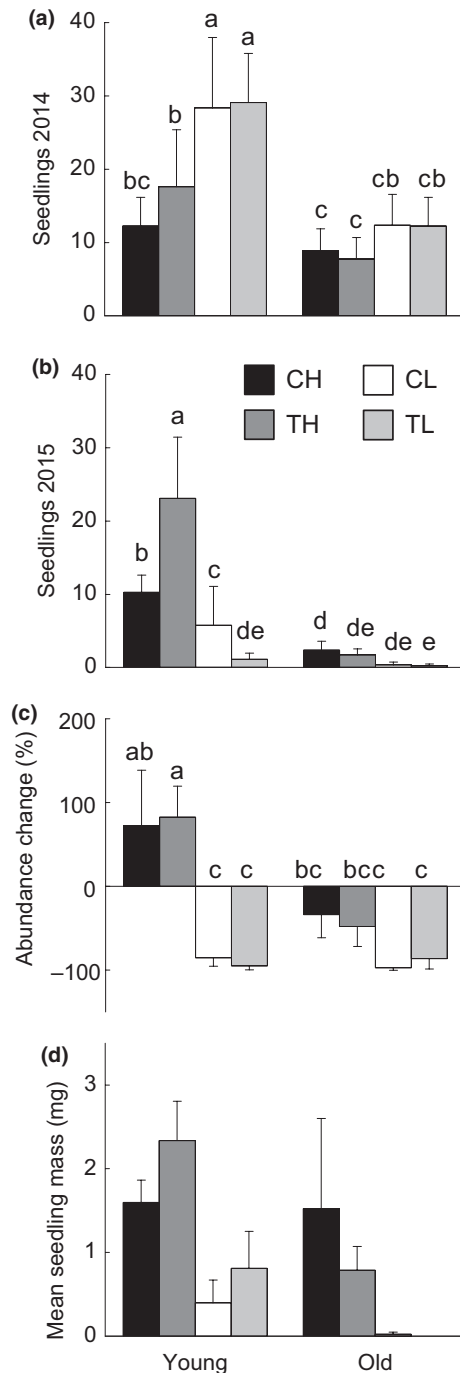
FIGURE 2 Outcomes of the transplantation experiment. Mean seedling numbers in 2014 (a), 2015 (b), relative change in seedling abundance (c), and mean seedling mass (d) in the different transplantation treatments (CH; control at high elevation, CL; control at low elevation, TH; transplanted to high elevation, TL; transplanted to low elevation) in the recent and old turfs. Error bars are standard errors, letters indicate significant differences between treatments. Raw data can be found in Appendix 2

the plots were flooded at least once in two consecutive years before sampling in 2013 (56%) and 2014 (67%) (Appendix S2). Other environmental conditions are described in Nilsson et al. (2017). Average growing season length (number of days with temperatures >5°C) across

field sites was 140.7 ± 2.45 days. Mean air temperature during the study period was 1.67 (range: 0.81–2.82), and mean day temperatures reached maxima of 18.2°C in 2012, 19.0°C in 2013 and 22.7°C in 2014.

3.4 | Recruitment in the seedling survey

In 2013 and 2014, we observed significantly different seedling numbers in the different flooding categories (GLMM; $\chi^2 = 4971.4$, $p < 0.001$ and $\chi^2 = 74.70$, $p < 0.001$ for 2013 and 2014 respectively). In 2013, we observed that flooding history of the previous season (i.e., 2012) modulated the number of seedlings in plots that had a similar flooding regime in 2013 (Figure 4). That is, significantly more seedlings were found in the FD plots compared to the DD plots (Tukey post-hoc z-ratio = −7.12, $p < 0.001$), while the flooding duration in 2013 was comparable among those treatments (12 days difference, Tukey post–hoc t-ratio = −1.42 $p = 0.487$, Figure 4b). Significantly less seedlings were found in the DF treatments compared to the FF treatment (z-ratio = −4.88, $p < 0.001$), despite the flooding duration in the year of the survey (2013) not being significantly different (seven days difference; Tukey post-hoc, t = −1.42, $p = 0.490$, Figure 4b). In the seedling survey of 2014, when (early) summer was extremely warm, the difference in seedling numbers between flooding-history categories reflected the flooding conditions of the survey year (2014), with more seedlings in the DF and the FF plots compared to the DD and FD plots (Figure 4).

When looking at the relation between time since the last flood and seedling densities in the plots in 2013 and 2014, variation is large, both at high and low elevations (Figure 5). What is very clear is that plots that were flooded during the winter preceding the seedling survey generally had few seedlings. Higher seedling numbers occurred predominantly in non-flooded plots and plots that were flooded ca. 50–100 days before the seedling survey (Figure 5). The correlation between seedling numbers and (log-transformed) days since the last flood was neither significant for 2013 (Pearson r = −0.13, df = 183, $p = 0.073$) nor for 2014 (r = −0.13, df = 186, $p = 0.069$).

4 | DISCUSSION

In our turf transplantation experiment, legacy effects of transplantation were not observed until the second year, or more importantly, after the first spring flood. At that time, we found large differences between transplanted and control turfs. In the 2013 seedling survey, differences between plots reflected the patterns observed in the transplantation experiment. In 2014, however, differences between flooding history categories merely reflected the wetness gradient of the summer in which the survey was carried out. Seedling numbers were low for plots flooded during the previous winter and did not correlate with the duration of the post-flood period. This shows that previous floods can affect recruitment in riparian zones via legacy effects and/or timing of the flood event (Sarneel et al., 2016; van Leeuwen, Sarneel, van Paassen, Rip, & Bakker, 2014), but also that
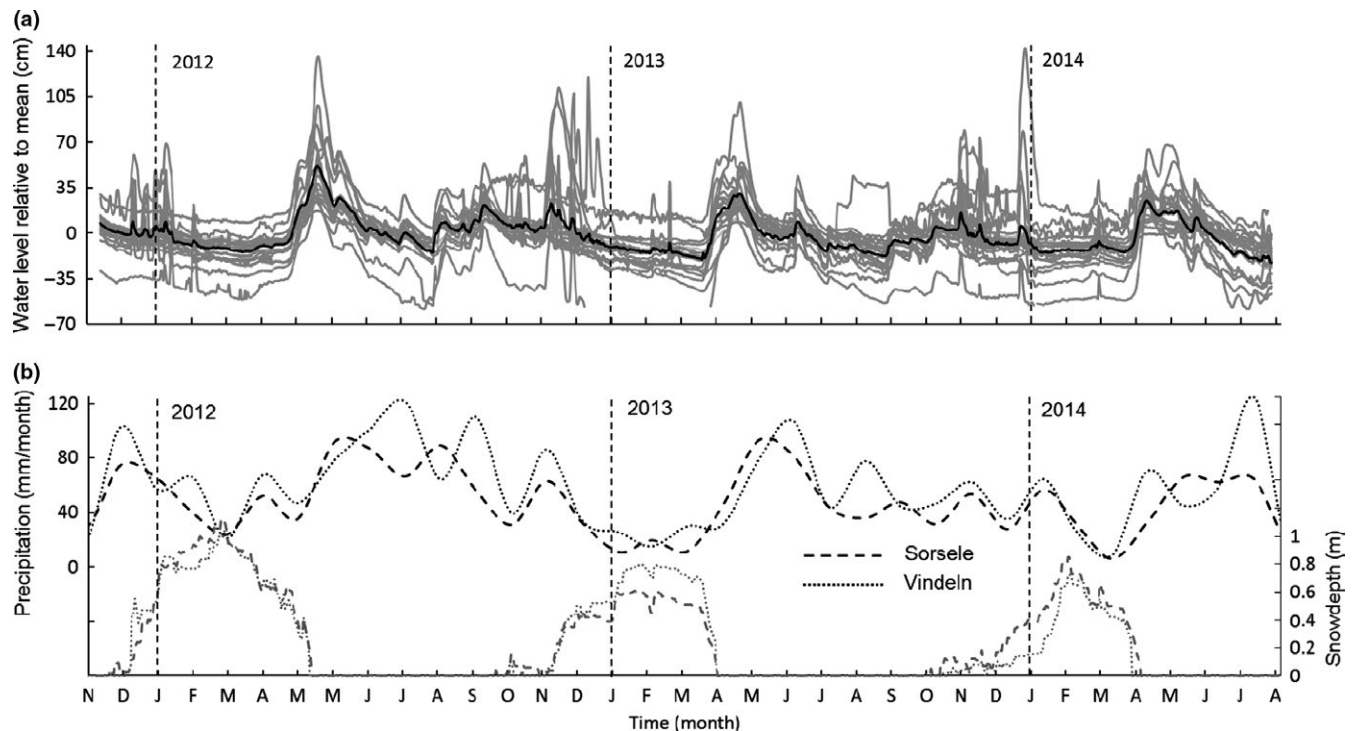
FIGURE 3 Flooding dynamics (a) in the 19 sampled reaches (grey) in three consecutive years, standardized around the mean water level, relative to the mean water level (black line). (b) Precipitation (black dashed lines) and snow accumulation (dark grey dashed lines) in Sorsele (65.5354° N; 17.5225° E) and Vindeln (64.1386° N; 19.7618° E) that represent the northern- and southern-most field location, respectively. Vindeln is 32 km southeast from the transplantation experiment in Strycksele. Data obtained from the SMHI open data database

flood history may interact with other climatic factors since patterns were not consistent between years.

4.1 | Legacy effects of long-term and recent flooding history

We observed opposite effects of long-term flooding histories between turfs transplanted to low and high elevations. This difference may depend on the death of less-adapted species and colonisation by better-adapted species (Sarneel et al., 2019). When mortality exceeds colonisation, bare ground may become available. As a matter of fact, we observed a dieback of vegetation after transplantation, while the dieback in the rotated control plots was negligible. Vegetation dieback was largest in the turfs that were moved to low elevation, where the vegetation was adapted to previous low-flooding frequencies. At high elevation, dieback may have decreased competition for light, which may have enhanced recruitment (Kotowski et al., 2010; Lenssen, Menting, & Van der Putten, 2003). At low elevation, in contrast, tolerance is thought to be a more important structuring force than competition. Therefore, vegetation dieback at low elevation may have reduced the sheltering effect that high stem densities provide against erosion and other mechanic stress during flooding, causing seedling mortality (Balke et al., 2014). Ström et al. (2011), who started the turf transplantation experiment, observed that the transplanted turfs reached a standing biomass similar to their receiving elevation

within five years after transplantation. We therefore hypothesised that if the observed legacy effects of transplantation are mediated by vegetation density, they may persist during a similar or shorter period. Therefore, after restoration, the arrival of seeds of desired species within a relatively short timeframe may be critical, especially in the higher parts of the floodplain where recruitment is temporarily enhanced after transplantation (Kotowski et al., 2010; Sarneel et al., 2016). In addition, legacies could exist in the composition and viability of the seed bank, which may differ at different locations along a riparian gradient (Bourgeois et al., 2017; Goodson et al., 2001; Grandin & Rydin, 1998). It remains to be seen, however, if such legacy effects on recruitment are sufficiently strong to drive vegetation composition (Sarneel et al., 2019), or if most species do not manage to arrive in time or establish within this window of opportunity (Balke et al., 2014; Hasselquist et al., 2015; Sarneel et al., 2014).

Although the setup of our field seedling survey was not ideal to test the occurrence of legacy effects directly, we found similar patterns between flood-history categories in the experiment and in the seedling survey in 2013. This suggests that past flooding events could result in legacy effects affecting seedling numbers under natural conditions in the field. In 2013, seedling numbers differed between plots with a different flooding history and a comparable flood duration in the latest year. In 2014, however, patterns shifted to reflect the conditions during the latest year. Since 2014 was characterised by a rather dry early summer, water stress may have overruled other
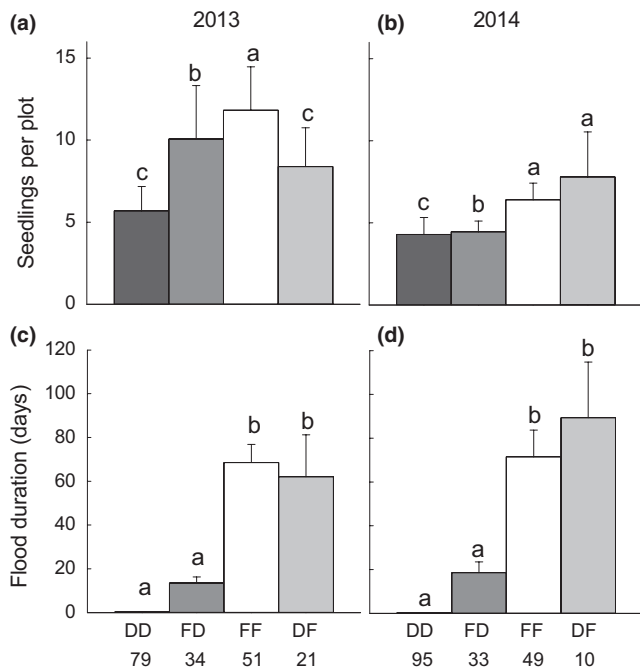
(a) 2013 **(b)** 2014

(c) **(d)**

DD 79 FD 34 FF 51 DF 21

DD 95 FD 33 FF 49 DF 10

FIGURE 4 Flooding categories. Number of seedlings per plot (a, b) in the field in plots with a different flooding history and the summed flooding duration in these plots (c, d) in the year of the seedling survey for 2013 (a, c) and 2014 (b, c). The first letter in the label indicates whether the plot had been dry (D) or flooded (F) in the year before the seedling counts were done, and the second letter for the year of the count. Numbers below the categories indicate number of plots within this category

drivers, indicating that the relative strength of different factors that determine recruitment may differ between years, and that more research is needed to entail the importance of legacy effects in natural field conditions.

4.2 | Importance of past flooding events

Especially long-term and frequent floods can provide major constraints on plant growth (e.g., anoxia, low light availability and physical stress of the water flow and sediment deposition; Bornette &

Puijalon, 2011). However, next to that, flooding events also provide moisture and seeds, which may increase recruitment. In contrast, absence of flooding may provide long recruitment periods that allow seedlings to grow large enough to survive future flooding events and thereby increase seedling numbers (Fraaije et al., 2015; Mahoney & Rood, 1998; Sarneel et al., 2014). These opposite effects of flooding occur at different time spans, and can explain why we found the drastic change in seedling densities in the transplantation experiment. There, seedling densities were first correlated with soil moisture and later with survival to flooding. Since the spring flood in 2015 was rather average, these observations also indicate that one growing season is unlikely to provide a disturbance-free recruitment window that is long enough for plants to reach a flood-resistant size.

In the seedling survey, we did not find support for our hypothesis that longer recruitment windows would result in higher seedling densities. Rather than finding an increase in seedling number with longer disturbance-free time periods in which recruitment can take place, we found a strong negative effect of winter floods (at moderately long recruitment windows). Higher seedling numbers were found in plots that were flooded during spring or not flooded during the test period. Since one growing season may likely be too short for seedlings to establish successfully, we assume that the majority of the seedlings that were found in plots with a recruitment window of 30–100 days will not establish but die during the next flood (Dixon, 2003; Fraaije et al., 2015). This factor may have obscured the relationship between seedling recruitment and the duration of the recruitment window.

The low number of seedlings in plots flooded during winter can be the consequence of not having the high seed input and soil moisture that short recruitment windows have, nor the high probability of recruitment that may drive high seedling numbers in plots with long recruitment windows. Rather than the best of two worlds, seedlings may encounter the worst of two worlds. In addition, winter flooding may be extremely detrimental in boreal zones as it often involves severe mechanical disturbance by ice, freezing and hyper-cooling (Lind, Nilsson, Polvi, & Weber, 2014; Rood, Goater, Mahoney, Pearce, & Smith, 2007; Smith & Pearce, 2000). In
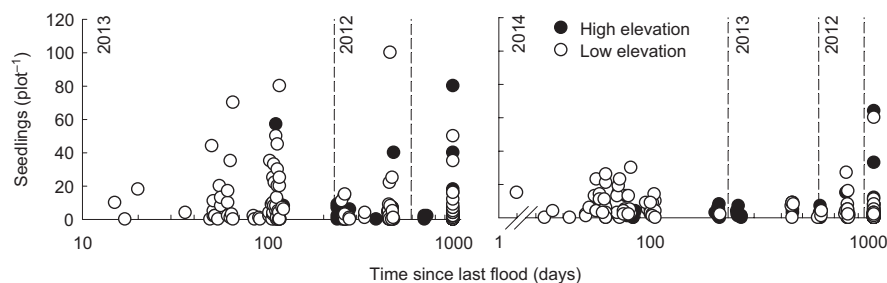

FIGURE 5 Numbers of seedlings in 50 cm × 100 cm field plots at high and low elevation (50 cm above or below mean water level, resp.) in August 2013 and 2014 in relation to the number of days since the last flooding event. Dashed lines indicate the first day of the year, with the plots that were never flooded during the study period given a fixed number of 1000

temperate zones, therefore, winter flooding may be less detrimental for plant growth and survival (Beumer et al., 2008; van Eck et al., 2006), and more studies in other climatic regions will increase our understanding further.

5 | CONCLUDING REMARKS

Both the long-term and the short-term flooding histories can affect plant recruitment, with consequences for restoration activities involving flood management. When restoration activities include introduction of seeds and other propagules to favour desired species, our results imply that these will be more successful in cases of decreased, compared to increased flooding regimes (van Leeuwen et al., 2014), and that there is likely only a short period in which the invasibility or colonisation is relatively high, at least for the type of species that we tested. Due to the low germination of *Carex*, the species represented the vegetation from intermediate to high elevations. However, given the strong negative impact of flooding across species in our system, we speculate that the study results thus point towards a low importance of species identity during the establishment phase in our systems, thus opposing findings in temperate streams (Fraaije et al., 2015; Sarneel et al., 2014).

At high elevation, where flooding frequencies were low, on average 4 and 1.87 new species appeared in transplanted and control turfs, respectively (data from Ström et al., 2011). Curiously, these numbers match the doubling of the seedling numbers when comparing transplanted and control turfs. Although seed input and diversity are often found to correlate positively in dispersal studies, studies on longer temporal and larger spatial scales are needed to further advance our understanding of the importance of recruitment for diversity (Andersson, Nilsson, & Johansson, 2000; Lenssen, Menting, van der Putten, & Blom, 1999). In our study system, however, it is likely that the low recruitment at low elevation is in line with the dominance of long-lived, clonal spreaders that likely makes them less dependent on recruitment from seeds and allows them to persist in habitats with frequent disturbance and a small window of opportunity for recruitment.

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AUTHOR CONTRIBUTIONS

JMS and CN conceived the study, JMS and MvO conducted the practical work and the statistical analysis. All authors contributed actively to writing.

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REFERENCES

Andersson, E., Nilsson, C., & Johansson, M. E. (2000). Plant dispersal in boreal rivers and its relation to the diversity of riparian flora. *Journal of Biogeography*, *27*, 1095–1106. https://doi.org/10.1046/j.1365-2699.2000.00481.x

Balke, T., Herman, P. M. J., & Bouma, T. J. (2014). Critical transitions in disturbance-driven ecosystems: Identifying Windows of Opportunity for recovery. *Journal of Ecology*, *102*, 700–708. https://doi.org/10.1111/1365-2745.12241

Beauchamp, V. B. & Stromberg, J. C. (2007). Flow regulation of the Verde River, Arizona encourages *Tamarix* recruitment but has minimal effect on *Populus* and *Salix* stand density. *Wetlands*, *27*, 381–389. https://doi.org/10.1672/0277-5212(2007)27[381:FROTVR]2.0.CO;2

Beumer, V., van Wirdum, G., Beltman, B., Griffioen, J., Grootjans, A. P., & Verhoeven, J. T. A. (2008). Geochemistry and flooding as determining factors of plant species composition in Dutch winter-flooded riverine grasslands. *Science of the Total Environment*, *402*, 70–81. https://doi.org/10.1016/j.scitotenv.2008.03.044

Bornette, G. & Puijalon, S. (2011). Response of aquatic plants to abiotic factors: a review. *Aquatic Sciences*, *73*, 1–14. https://doi.org/10.1007/s00027-010-0162-7

Bourgeois, B., Boutin, C., Vanasse, A., & Poulin, M. (2017). Divergence between riparian seed banks and standing vegetation increases along successional trajectories. *Journal of Vegetation Science*, *28*, 787–797. https://doi.org/10.1111/jvs.12536

Bourgeois, B., Gonzalez, E., Vanasse, A., Aubin, I., & Poulin, M. (2016). Spatial processes structuring riparian plant communities in agroecosystems: implications for restoration. *Ecological Applications*, *26*, 2103–2115. https://doi.org/10.1890/15-1368.1

Braatne, J. H., Jamieson, R., Gill, K. M., & Rood, S. B. (2007). Instream flows and the decline of riparian cottonwoods along the Yakima River, Washington, USA. *River Research and Applications*, *23*, 247–267. https://doi.org/10.1002/rra.978

Crawley, M. J. (2007). *The R book*. Chichester: Wiley.

Dixon, M. D. (2003). Effects of flow pattern on riparian seedling recruitment on sandbars in the Wisconsin River, Wisconsin, USA. *Wetlands*, *23*, 125–139. https://doi.org/10.1672/0277-5212(2003)023[0125:eofpor]2.0.co;2

Fraaije, R. G. A., ter Braak, C. J. F., Verduyn, B., Verhoeven, J. T. A., & Soons, M. B. (2015). Dispersal versus environmental filtering in a dynamic system: drivers of vegetation patterns and diversity along stream riparian gradients. *Journal of Ecology*, *103*, 1634–1646. https://doi.org/10.1111/1365-2745.12460

Fukami, T. (2015). Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 1–23. https://doi.org/10.1146/annurev-ecolsys-110411-160340

Garssen, A. G., Baattrup-Pedersen, A., Voesenek, L. A. C. J., Verhoeven, J. T. A., & Soons, M. B. (2015). Riparian plant community responses to increased flooding: a meta-analysis. *Global Change Biology*, *21*, 2881–2890. https://doi.org/10.1111/gcb.12921

Goodson, J. M., Gurnell, A. M., Angold, P. G., & Morrissey, I. P. (2001). Riparian seed banks: Structure, process and implications for riparian management. *Progress in Physical Geography*, *25*, 301–325. https://doi.org/10.1016/s0169-555x(02)00140-x

Grandin, U. & Rydin, H. (1998). Attributes of the seed bank after a century of primary succession on islands in Lake Hjälmaren,

Sweden. *Journal of Ecology*, *86*, 293–303. https://doi.org/10.1046/j.1365-2745.1998.00252.x

Greene, S. L., & Knox, J. C. (2014). Coupling legacy geomorphic surface facies to riparian vegetation: Assessing red cedar invasion along the Missouri River downstream of Gavins Point dam, South Dakota. *Geomorphology*, *204*, 277–286. https://doi.org/10.1016/j.geomorph.2013.08.012

Hasselquist, E. M., Nilsson, C., Hjältén, J., Jørgensen, D., Lind, L., & Polvi, L. E. (2015). Time for recovery of riparian plants in restored northern Swedish streams: A chronosequence study. *Ecological Applications*, *25*, 1373–1389. https://doi.org/10.1890/14-1102.1

Hennekens, S. M., Smits, N. A. C., & Schaminée, J. H. J. (2010). *SynbioSys Nederland*, version 2. Wageningen, The Netherlands: Alterra.

Herberg, E. R. & Sarneel, J. M. (2017). Recruitment of riparian plants after restoration of geomorphic complexity in northern Sweden. *Journal of Applied Vegetation Science*, *20*, 435–445. https://doi.org/10.1111/avsc.12304

Hirabayashi, Y., Mahendran, R., Koirala, S., Konoshima, L., Yamazaki, D., Watanabe, S., ... Kanae, S. (2013). Global flood risk under climate change. *Nature Climate Change*, *3*, 816–821. https://doi.org/10.1038/nclimate1911

Kotowski, W., Beauchard, O., Opdekamp, W., Meire, P., & van Diggelen, R. (2010). Waterlogging and canopy interact to control species recruitment in floodplains. *Functional Ecology*, *24*, 918–926. https://doi.org/10.1111/j.1365-2435.2009.01682.x

Lenssen, J. P. M., Menting, F. B. J., & Van der Putten, W. H. (2003). Plant responses to simultaneous stress of waterlogging and shade: amplified or hierarchical effects? *New Phytologist*, *157*, 281–290. https://doi.org/10.1046/j.1469-8137.2003.00666.x

Lenssen, J. P. M., Menting, F. B. J., van der Putten, W. H., & Blom, C. W. P. M. (1999). Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. *Oikos*, *86*, 523–534. https://doi.org/10.2307/3546656

Lenth, R. V. (2016). Least-squares means: The R package lsmeans. *Journal of Statistical Software*, *69*. https://doi.org/10.18637/jss.v069.i01

Levine, C. M. & Stromberg, J. C. (2001). Effects of flooding on native and exotic plant seedlings: implications for restoring south-western riparian forests by manipulating water and sediment flows. *Journal of Arid Environments*, *49*, 111–131. https://doi.org/10.1006/jare.2001.0837

Li, S., & Pennings, S. C. (2016). Disturbance in Georgia salt marshes: variation across space and time. *Ecosphere*, *7*, e01487. https://doi.org/10.1002/ecs2.1487

Lind, L., Nilsson, C., Polvi, L. E., & Weber, C. (2014). The role of ice dynamics in shaping vegetation in flowing waters. *Biological Reviews*, *89*, 791–804. https://doi.org/10.1111/brv.12077

Luo, F.-L., Huang, L., Lei, T., Xue, W., Li, H.-L., Yu, F.-H., & Cornelissen, J. H. C. (2016). Responsiveness of performance and morphological traits to experimental submergence predicts field distribution pattern of wetland plants. *Journal of Vegetation Science*, *27*, 340–351. https://doi.org/10.1111/jvs.12352

Mahoney, J. M., & Rood, S. B. (1998). Streamflow requirements for cottonwood seedling recruitmen — an integrative model. *Wetlands*, *18*, 634–645. https://doi.org/10.1007/bf03161678

Menge, B. A., & Sutherland, J. P. (1987). Community regulation: Variation in disturbance, competition, and predation in relation to environmental-stress and recruitment. *American Naturalist*, *130*, 730–757. https://doi.org/10.1086/284741

Merritt, D. M., Nilsson, C., & Jansson, R. (2010). Consequences of propagule dispersal and river fragmentation for riparian plant community diversity and turnover. *Ecological Monographs*, *80*, 609–626. https://doi.org/10.1890/09-1533.1

Naiman, R. J., & Décamps, H. (1997). The ecology of interfaces: riparian zones. *Annual Review of Ecology and Systematics*, *28*, 621–658. https://doi.org/10.1146/annurev.ecolsys.28.1.621

Nilsson, C., Jansson, R., & Zinko, U. (1997). Long-term responses of river-margin vegetation to water-level regulation. *Science*, *276*, 798–800. https://doi.org/10.1126/science.276.5313.798

Nilsson, C., Reidy, C. A., Dynesius, M., & Revenga, C. (2005). Fragmentation and flow regulation of the world's large river systems. *Science*, *308*, 405–408. https://doi.org/10.1126/science.1107887

Nilsson, C., Riis, T., Sarneel, J. M., & Svavarsdóttir, K. (2018). Ecological restoration as a means of managing inland flood hazards. *BioScience*, *68*, 89–99. https://doi.org/10.1093/biosci/bix148

Nilsson, C., Sarneel, J. M., Palm, D., Gardeström, J., Pilotto, F., Polvi, L. E., ... Lundqvist, H. (2017). How do biota respond to additional physical restoration of restored streams. *Ecosystems*, *20*, 144–162. https://doi.org/10.1007/s10021-016-0020-0

Pennings, S. C. & Callaway, R. M. (1992). Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology*, *73*, 681–690. https://doi.org/10.2307/1940774

Rankin, W. T., & Pickett, S. T. A. (1989). Time of establishment of red maple (*Acer rubrum*) in early oldfield succession. *Bulletin of the Torrey Botanical Club*, *116*, 182–186. https://doi.org/10.2307/2997200

Rood, S. B., Goater, L. A., Mahoney, J. M., Pearce, C. M., & Smith, D. G. (2007). Floods, fire, and ice: disturbance ecology of riparian cottonwoods. *Canadian Journal of Botany-Revue Canadienne De Botanique*, *85*, 1019–1032. https://doi.org/10.1139/b07-073

Sarneel, J. M., Hefting, M. M., Kowalchuk, G. A., Nilsson, C., Van der Velden, M., Visser, E. J. W., ... Jansson, R. (2019). Alternative transient states and slow plant community responses after changed flooding regimes. *Global Change Biology*, https://doi.org/10.1111/gcb.14569.

Sarneel, J. M., Janssen, R. H., Rip, W. J., Bender, I. M. A., & Bakker, E. S. (2014). Windows of opportunity for germination of riparian species after restoring water level fluctuations: a field experiment with controlled seed banks. *Journal of Applied Ecology*, *51*, 1006–1014. https://doi.org/10.1111/1365-2664.12288

Sarneel, J. M., Kardol, P., & Nilsson, C. (2016). The importance of priority effects for riparian plant community dynamics. *Journal of Vegetation Science*, *27*, 658–667. https://doi.org/10.1111/jvs.12412

Smith, D. G., & Pearce, C. M. (2000). River ice and its role in limiting woodland development on a sandy braid-plain, Milk River, Montana. *Wetlands*, *20*, 232–250. https://doi.org/10.1672/0277-5212(2000)020[0232:riairi]2.0.co;2

Soomers, H., Sarneel, J. M., Patberg, W., Verbeek, S. K., Verweij, P. A., Wassen, M. J., & van Diggelen, R. (2011). Factors influencing the seed source and sink functions of a floodplain nature reserve in the Netherlands. *Journal of Vegetation Science*, *22*, 445–456. https://doi.org/10.1111/j.1654-1103.2011.01261.x

Ström, L., Jansson, R., Nilsson, C., Johansson, M. E., & Xiong, S. (2011). Hydrologic effects on riparian vegetation in a boreal river: an experiment testing climate change predictions. *Global Change Biology*, *17*, 254–267. https://doi.org/10.1111/j.1365-2486.2010.02230.x

van Eck, W. H. J. M., Lenssen, J. P. M., van de Steeg, H. M., Blom, C. P. W. M., & de Kroon, H. (2006). Seasonal dependent effects of flooding on plant species survival and zonation: a comparative study of 10 terrestrial grassland species. *Hydrobiologia*, *565*, 59–69. https://doi.org/10.1007/s10750-005-1905-7

Van Eck, W. H. J. M., Van De Steeg, H. M., Blom, C. W. P. M., & De Kroon, H. (2004). Is tolerance to summer flooding correlated with distribution patterns in river floodplains? A comparative study of 20 terrestrial grassland species. *Oikos*, *107*, 393–405. https://doi.org/10.1111/j.0030-1299.2004.13083.x

van Leeuwen, C. H. A., Sarneel, J. M., van Paassen, J., Rip, W. J., & Bakker, E. S. (2014). Hydrology, shore morphology and species traits affect seed dispersal, germination and community assembly in shoreline plant communities. *Journal of Ecology*, *102*, 998–1007. https://doi.org/10.1111/1365-2745.12250

Winemiller, K. O., McIntyre, P. B., Castello, L., Fluet-Chouinard, E., Giarrizzo, T., Nam, S., ... Sáenz, L. (2016). Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science*, *351*, 128–129. https://doi.org/10.1126/science.aac7082

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1 Germination in the transplantation experiment per species

Appendix S2 Data of the transplantation experiment and field survey