



The importance of priority effects for riparian plant community dynamics

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Keywords

Community assembly; Community dynamics; Dispersal vector; Historical contingency; Hydrochory; Invasibility; Niche space; Plant population; Stream ecology; Succession

Abbreviations

BS = Species group consisting of *Betula pubescens* and *Solidago virgaurea*;
FMP = Species group consisting of *Filipendula ulmaria*, *Molinia caerulea* and *Prunella vulgaris*.

Nomenclature

Mossberg & Stenberg (2010)

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Introduction

Vegetation composition is often seen as a result of filtering by dispersal, environmental conditions and biotic interactions. However, stochastic factors, such as the arrival

Abstract

Questions: The order of plant species arrival can affect recruitment and subsequent plant community development via priority effects, but is often overlooked. Priority effects occur when early-colonizing plant species affect the establishment of later-arriving species, and are hypothesized to depend on species identity and habitat conditions. In riparian ecosystems on the banks of rivers, a strong moisture gradient induces a zonation of plant species with different degrees of adaptation to soil moisture. Further, riparian zones receive seeds during floods and later in the season via wind dispersal. As such, we questioned if recruitment in riparian zones is primarily affected by (1) environmental conditions (i.e. soil moisture), (2) arrival order, and (3) species identity, or an interaction between these factors.

Location: Riparian zones of tributaries in the Vindel River catchment, northern Sweden.

Method: We designed a controlled greenhouse experiment and a large-scale field experiment where we sowed five plant species representing different dispersal events and habitat moisture preferences. We sowed seeds in three arrival order treatments (all species simultaneously, species group A phased 3 wk before group B, and *vice versa*) and under different soil moisture treatments in the greenhouse (dry, dry-after-wet and wet) and under a range of moisture conditions in the field.

Results: We found strong priority effects as early-arriving species grew bigger and often produced higher seedling densities compared to later-arriving species, both in the greenhouse and after two growing seasons in the field. Priority effects in the greenhouse were strongest in the dry and dry-after-wet treatments and weaker under wet conditions. Consistent but weaker patterns were observed in the field after the first growing season. The relative abundance of species in plant communities assembled without phased arrival interacted with soil moisture and species identity. Priority effects were strongest for species with a low relative abundance (i.e. less competitive species).

Conclusions: Our findings that priority effects influenced recruitment and interacted with soil moisture suggest that priority effects should be considered when addressing riparian vegetation changes after shifts in flooding regimes. This is especially important because floods will not only affect habitat conditions, but also the phasing of seed arrival.

history of species, can have a strong modulating effect on community assembly through priority effects (Drake 1991; Weiher & Keddy 1995; Chase 2003; Ejrnæs et al. 2006). That is, early-arriving species are the first to use the available resources such as light and nutrients (Vannette &

Fukami 2014), and can induce changes through which they can gain a competitive advantage over later-arriving species (Hausmann & Hawkes 2009). Benign environments that stimulate growth can increase competitive advantage of early-arriving over late-arriving species and thereby strengthen priority effects (Ejrnæs et al. 2006; Kardol et al. 2013). For example, species-specific patterns of resource acquisition have been shown to correlate with the strength of priority effects in yeast communities (Vannette & Fukami 2014). Priority effects may thus allow less competitive species that arrive early to persist when dominant species arrive later, and resources that influence a species' competitive strength should drive priority effects. This suggests a strong potential for interactions between arrival history and environmental filtering. However, there is no consensus on when and how priority effects occur or how they interact with habitat or life-history traits, especially under field conditions (Fukami et al. 2005; Vannette & Fukami 2014; Cleland et al. 2015). Yet, improved understanding of priority effects is important as it has clear implications for restoration and invasion ecology (Cleland et al. 2015).

Riparian ecosystems occupy the interface between water and land and represent a dynamic environment harbouring species that are adapted to different degrees of flooding, each at their own specific elevation (Nilsson & Svedmark 2002). These factors make these ecosystems hotspots of biodiversity in the landscape (Nilsson & Svedmark 2002). In boreal zones, the majority of dispersed seeds and other propagules arrive in these systems through the spring flood, which in northern latitudes occurs in late May or early Jun, a few weeks after snow melt. Dispersal by other vectors, such as water birds (Figuerola & Green 2002) and wind (Merritt et al. 2010; Sarneel et al. 2014), provides seeds to riparian zones during other periods of the year, although in lower numbers (Boedeltje et al. 2004; Merritt et al. 2010). It has been suggested that wind- and water-dispersed species may have different probabilities to establish along the wetness gradient in riparian systems (Merritt et al. 2010), and that both dispersal limitations and establishment limitations shape the vegetation zonation (Sarneel et al. 2014; Fraaije et al. 2015).

Soil moisture and water level fluctuations are the main environmental variables shaping the riparian zone as they strongly affect seed germination, seedling survival and plant growth (Sarneel et al. 2014; Fraaije et al. 2015). In addition to strong direct effects through environmental filtering, soil moisture may also indirectly affect community assembly by modulating priority effects. For example, Martin & Wilsey (2014) observed a significant interaction between arrival order and soil type on prairie grassland community composition (i.e. larger differences between sowing treatments in dry sand vs moist organic substrate).

Further, Foster & Dickson (2004) found that irrigation increased vegetation cover only in grassland plots that had received additional seeds of 32 local species. Recently, Young et al. (2015) observed location-specific effects of irrigation on the prior establishment of native species. Lastly, Moore & Franklin (2012) found that priority effects interacted with soil moisture for seedlings of *Panicum capillare* and *Polygonum persicaria* in a complex manner, determining interactions between two individual plants.

In summary, riparian systems receive mixtures of seeds of species with different abiotic preferences sequentially arriving during the season. Whether priority effects play a role in recruitment success in riparian vegetation and how priority effects would interact with soil moisture or species identity (strategy to deal with moisture) has been debated but rarely addressed empirically. This makes the riparian system ideal for testing interactions of environmental conditions, species identity and arrival order in driving seedling recruitment and community assembly. Here, we ran a controlled greenhouse experiment and a large-scale field experiment in the Vindel River catchment in northern Sweden to test the occurrence of priority effects and the interaction with life-history traits and habitat conditions. We hypothesized (1) that early-arriving species would negatively affect the establishment of later-arriving species, and as such alter plant community composition, and (2) that priority effects would interact with soil moisture. As moist soils are favourable for most riparian species, we expected priority effects to be stronger under wet than under dry conditions. Lastly, we hypothesized (3) that species performance (depending on species identity and soil moisture) would determine the strength of priority effects, with well-performing species being less affected by priority effects than species that perform less well.

Methods

A greenhouse experiment and a field experiment were conducted with five riparian plant species (Appendix S1 for details). Based on results from Merritt et al. (2010), we selected *Filipendula ulmaria* L., *Molinia caerulea* L. and *Prunella vulgaris* L. (together referred to as *FMP*) as species that are dispersed by floodwater, primarily during the spring, and *Betula pubescens* Ehrh. and *Solidago virgaurea* L. (together referred to as *BS*) as species dispersed by other means. These two species groups thus represent two arrival events in our system. *Solidago* and *Prunella* are typical for drier parts of the riparian zones, whereas the other species are typically found closer to the water. Seeds were obtained from commercial seed companies (Appendix S1). The selected streams are characterized by undisturbed glacial legacy sediment (Appendix S2) and have a growing season (day temperature >5 °C) of ca. 150 d.

Greenhouse experiment

In the greenhouse we used a randomized full-factorial design (Fig. 1) with six replicates per treatment and tested three soil moisture treatments (dry, dry-after-wet, wet) and three different arrival orders: (1) all species sown simultaneously (hereafter referred to as Control), (2) first the group with *Betula* and *Solidago* (*BS*) then the group containing *Filipendula*, *Molinia* and *Prunella* (*FMP*) (hereafter referred to as *BS* first), and (3) first the group *FMP* then the group *BS* (hereafter referred to as *FMP* first). Pots (13-cm diameter, 9-cm height) were filled with potting mix (10% sand, 90% organic soil; Rölunda produkter, Bålsta, SE) and placed in bigger trays (four pots per tray). In the dry treatment, pots were watered weekly with the amount corresponding to the mean weight loss of six pots ($138 \pm 9 \text{ ml} \pm \text{SE}$). For the wet and dry-after-wet treatments water was maintained 5 cm below the soil level (= field capacity, optimal for germination and establishment; Sarneel et al. 2014). To explicitly test for effects of environmental variability as it occurs in riparian systems, the water from the larger trays was removed after 3 wk in the dry-after-wet treatment. Thereafter the pots were watered weekly as in the dry treatment. Control treatments were sown at the start of the experiment with 45 seeds of each species in group *BS* and 30 seeds of each species in

group *FMP*, resulting in 90 seeds per group. In *BS* first treatments, *BS* seeds were sown 3 wk before *FMP* seeds, while in *FMP* first treatments, *FMP* seeds were sown 3 wk before *BS* seeds (Eriksson & Eriksson 1998; Kardol et al. 2013). Once a week, all pots (54 in total) were re-randomized over the greenhouse space. Mean greenhouse temperature was $21.9 \pm 0.25 \text{ }^\circ\text{C}$, light was provided 16 h-d^{-1} at a mean light intensity of $115 \pm 14 \text{ } \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

Seedling numbers and height were determined for each species 6 wk after sowing (i.e. 6 and 9 wk after the start of the experiment, respectively, for seeds sown first and second; Fig. 1). Nine weeks after the start of the experiment, all seedlings were counted, clipped at soil level, sorted to species, dried (48 h at $60 \text{ }^\circ\text{C}$) and weighed.

Field experiment

We cleared eight $40 \times 40 \text{ cm}$ plots in each of seven tributaries ($n = 56$) in the Vindel River catchment (Appendix S2) by removing litter, vegetation and large rhizomes after the spring flood in mid-Jun 2013. Each plot was divided into four $10 \times 10 \text{ cm}$ quadrats in which a block of four arrival order treatments was established. In control treatments, all five species were sown simultaneously. As we expected a lower germination in the field due to the cold climate, we applied more seeds here than in the greenhouse; i.e. $0.10 \text{ g}\cdot\text{species}^{-1}$, resulting in ca. 400 seeds per species group. In *BS* first treatments, *BS* seeds were sown 3 wk before *FMP* seeds, and in *FMP* first treatments, *FMP* seeds were sown 3 wk before *BS* seeds. No sowing treatment was applied to the fourth quadrat, but as the numbers of seedlings recruiting through natural colonization were negligible compared to the number of seedlings in sown plots (Appendix S3), we omitted this treatment from our analyses.

We counted the total number of seedlings after 3 wk (Jul 2013) and 9 wk (Aug 2013), and in Jun and Aug 2014. Upon each visit, we measured soil moisture of each treatment block using a ThetaProbe ML2x (Delta-T Devices, Burwell, UK). In Aug 2014, we collected the above-ground standing biomass separated into species groups of at least four replicate treatment blocks per tributary; the remaining replicates could not be harvested due to logistic constraints. Plant material was dried (48 h at $60 \text{ }^\circ\text{C}$) and weighed.

Calculations

For each pot in the greenhouse experiment and each quadrat in the field experiment we calculated the Shannon diversity index using the R package *vegan* (R Foundation for Statistical Computing, Vienna, AT). For the field quadrats we calculated seedling turnover as the difference

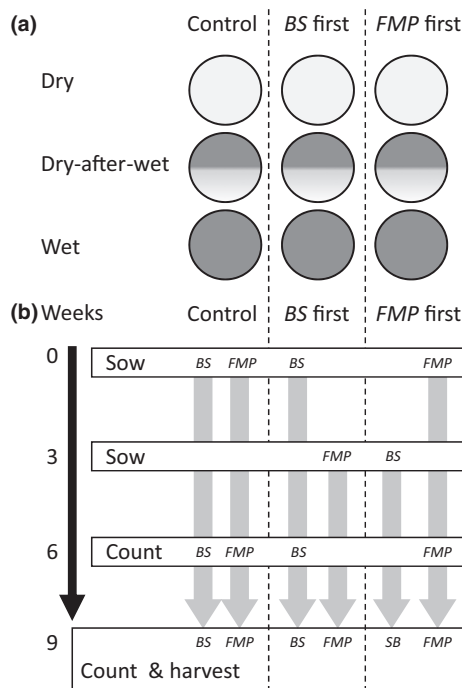


Fig. 1. Diagram showing (a) the full factorial design of soil moisture and arrival treatments and (b) sowing and counting intervals for each of the species groups. *BS* = *Betula* and *Solidago*, *FMP* = *Filipendula*, *Molinia* and *Prunella*.

between the number of seedlings in Aug 2013 and Aug 2014. The strength of priority effects (Eq. 1) was calculated as the natural logarithm of the ratio between the seedling numbers (D) of species $i + 1$, when it was sown after species j and when it was sown before species j ,

$$\text{Priority strength} = \ln(D(i_{ji})/D(i_{ij})) \quad (1)$$

where subscripts indicate the arrival order (Vannette & Fukami 2014). Positive values indicate facilitation and negative values indicate inhibitory priority effects. For the greenhouse experiment we used the number of seedlings 6 wk after sowing, and for the field experiment we used the number of seedlings after two growing seasons. As a measure of competitive strength, we calculated the relative growth rate (RGR) based on the height increase from 6 to 9 wk in the greenhouse control treatment. As a measure of species performance we calculated the relative abundance (Eq. 2) in the control treatments of both the greenhouse and the field experiment:

$$\text{Relative abundance} = D(i)/D(\text{tot}) \quad (2)$$

where $D(\text{tot})$ is the total number of seedlings in the control treatment. There was not much variation in seedling size in the field as there was a strong correlation between total mass and seedling number ($F_{1,57} = 52.1$, $P < 0.001$, $R^2 = 48\%$). As such, the measure of relative abundance integrates species responses to soil moisture with respect to germination, survival and competition.

Statistics

Treatment effects were tested for seedling number of *BS* and *FMP*, seedling height of *BS* and *FMP*, total community seedling number, above-ground biomass and Shannon diversity index in the greenhouse experiment. We used two-way ANOVAs with arrival order, soil moisture and their interaction as fixed effects.

To test for interactions between arrival order and soil moisture in the field experiment, we classified replicate plots with a mean soil moisture content $>40\%$ as wet (mean = $67 \pm 5.4\%$, $n = 19$), and $<40\%$ as dry (mean = 21 ± 1.3 , $n = 32$). This classification resulted in classes that did not significantly differ from the wet and dry treatments in the greenhouse experiment (71% and 23%, respectively). To obtain this, we omitted plots with a moisture content $<10\%$ ($n = 5$). For Aug 2014, some treatment quadrats of a few plots were omitted from the analyses because of disturbance by encroachment of neighbouring plants ($n = 11$; never more than one quadrat omitted per replicate plot).

In the field, to account for the block structure of our experiment and the sampling within seven different tributaries, seedling number per species group in Aug 2013 and 2014, species biomass per species group in Aug 2014, seedling turnover per species group, total seedling number in Aug 2013, Jun and Aug 2014, total above-ground biomass and Shannon diversity index were tested with repeated measures LMM. The arrival order treatments in the quadrats of one plot were addressed as repeats, and each plot was nested within its tributary. Soil moisture category and arrival order treatment and their interaction were used as fixed factors and tributary as a random factor. Parameters were tested for normal distribution and $\ln(x + 1)$ -transformed when necessary. A compound symmetry covariance structure was used as this gave the best fitting models.

To test the effect of arrival order over time, we performed repeated measures LMM, with treatment plots as subject factor and an unstructured covariance structure. Time, moisture and arrival order treatment and their interactions were used as fixed factors, while tributary was used as random factor. Bonferroni post-hoc tests were performed to test differences between treatments and time periods. Correlations between species performance and strength of priority effects were tested with a Pearson correlation. All analyses were conducted in IBM SPSS Statistics for Windows 22.0 (IBM, Armonk, New York, NY, US).

Results

Greenhouse experiment

We observed strong priority effects: seedling numbers and seedling height of 6-wk-old seedlings (i.e. 6 and 9 wk after the start of the experiment) were lower for species that arrived second (Fig. 2, Table 1). While the effects of priority on plant height were consistent among moisture treatments (Fig. 2, Table 1), priority effects interacted with soil moisture for seedling numbers (Table 1). Under dry (significant for *BS*, not for *FMP*) and dry-after-wet conditions (significant for *BS* and *FMP*) seedling numbers were lower for seeds arriving second (Fig. 2a,b, Table 1). In contrast, under wet conditions no priority effects were found for *BS* while *FMP* seedlings arriving second showed slightly increased germination rates (Fig. 2b). Trends were rather consistent across species within groups (Appendix S4), although *Molinia* and *Filipendula* germinated poorly (only in wet treatments) and therefore could not be analysed.

We also observed priority effects on the structure of the seedling community. The total number of seedlings was lower in treatments under phased arrival, and slightly increased under wet conditions (Fig. 3a, Table 1). Seedling numbers were more similar among arrival order

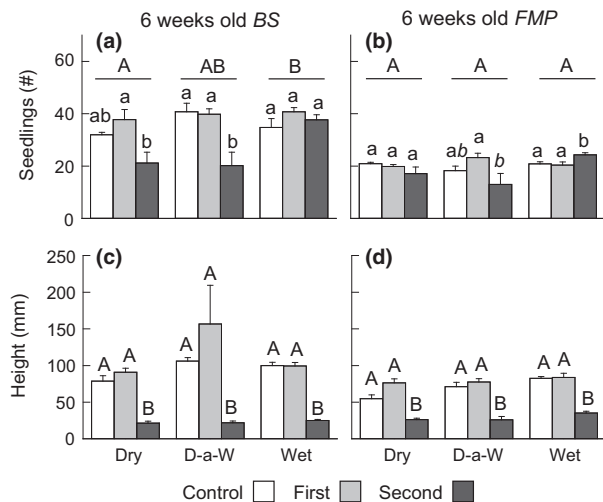


Fig. 2. Seedling performance in the greenhouse experiment. Seedling numbers (a, b) and height (c, d) 6 wk after sowing for BS and FMP seedling groups. Control: all species sown simultaneously; first: focal group first; second: focal group second. D-a-W: dry-after-wet soil moisture treatment. Data are means \pm SE. Uppercase letters indicate significant differences between main effects of moisture and arrival order treatments, and lowercase letters indicate differences within moisture treatments (Bonferroni, $P < 0.05$; italics for $P = 0.06$).

treatments under wet conditions compared to dry and dry-after-wet treatments, but the interaction was not significant (Table 1). Total standing biomass significantly

increased in wetter treatments (Fig. 3b, Table 1), but was not affected by seedling arrival order. The Shannon diversity index was significantly lower in treatments with phased arrival compared to the control, but diversity was not affected by soil moisture treatment and there was no interaction (Fig. 3c, Table 1).

Field experiment

All sown species successfully germinated. After one growing season (Aug 2013), arriving first increased germination rate of FMP seeds, but only under dry conditions (Fig. 4b), as indicated by a significant interaction between soil moisture and arrival order (Table 1). In Aug 2014, this interaction was no longer significant (Fig. 4b). In both years we observed more FMP seedlings under wet than under dry conditions (Table 1). The number of BS seedlings was not affected by arrival order or soil moisture in 2013 (Fig. 4a), but after two growing seasons, BS seedling numbers were marginally higher in BS first treatments compared to control and FMP first treatments (Fig. 4c, Table 1). Total biomass of the seedlings of each species group was significantly larger when sown first than when sown second (Fig. 4e,f, Table 1). No effects of soil moisture on seedling biomass were observed for either of the species groups (Table 1). The turnover of BS seedlings from 2013 to 2014 was negative and significantly lower when sown second

Table 1. Statistical results from the two-way ANOVAs and repeated measures LMMs. Effects of arrival order and soil moisture were tested on species responses and community composition in the greenhouse (GH). Repeated measures LMMs tested responses of the different species groups (BS and FMP) and community structure in the field (F).

	Arrival (A)			Moisture (M)			A \times M			
	df	F	P	df	F	P	df	F	P	
GH Seedlings BS	2	13.4	>0.001	2	4.05	0.024	4	3.79	0.010	
GH Seedlings FMP	2	1.83	0.173	2	2.86	0.068	4	3.69	0.011	
GH Seedling Height BS	2	30.2	>0.001	2	2.18	0.125	4	1.19	0.330	
GH Seedling Height FMP	2	52.6	>0.001	2	1.68	0.198	4	1.64	0.181	
GH Total Seedling Number	2	12.47	<0.001	2	8.28	0.001	4	1.25	0.305	
GH Total Standing Biomass	2	2.55	0.089	2	27.6	<0.001	4	0.73	0.575	
GH Shannon Diversity	2	1245	<0.001	2	2.81	0.071	4	1.40	0.248	
F Seedlings BS	2013	98	0.03	0.968	49	1.93	0.172	98	0.04	0.966
F Seedlings FMP	2013	98	0.98	0.380	47.8	7.92	0.007	98	4.81	0.010
F Seedlings BS	2014	92.8	2.92	0.059	48.8	0.00	0.990	92.8	0.32	0.730
F Seedlings FMP	2014	92.6	1.37	0.259	48.8	5.52	0.023	92.6	0.68	0.510
F Biomass BS	2014	35.6	5.56	0.008	19.3	0.01	0.913	35.6	0.14	0.872
F Biomass FMP	2014	35.6	7.70	0.002	19.5	1.75	0.201	35.6	0.48	0.622
F Seedling turnover BS	98	3.43	0.036	48.8	0.66	0.419	98	0.18	0.837	
F Seedling turnover FMP	93.4	0.74	0.481	48.7	0.96	0.332	93.4	0.42	0.657	
F Total seedlings Aug	2013	98	0.47	0.624	49	6.61	0.013	98	2.48	0.089
F Total seedlings Jun	2014	98	3.48	0.035	47.4	0.43	0.517	98	2.83	0.064
F Total seedlings Aug	2014	89.2	1.26	0.289	48.5	2.45	0.124	89.2	1.03	0.361
F Total biomass Aug	2014	35.3	4.42	0.019	19.5	1.31	0.267	35.2	0.61	0.548
F Diversity Aug	2013	96	1.83	0.167	47.6	10.67	0.002	96	0.62	0.539
F Diversity Aug	2014	92.4	2.68	0.074	48.8	3.15	0.082	92.4	0.31	0.737

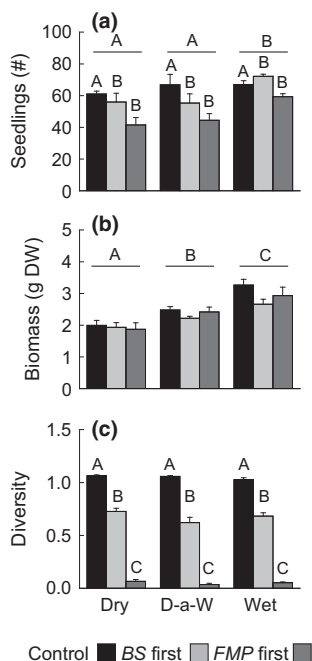


Fig. 3. Effects of arrival order (simultaneous arrival (Control), BS first and FMP first) and soil moisture treatments (Dry, Dry-after-Wet (D-a-W), Wet) on the total number of seedlings (a), total seedling biomass (b) and Shannon diversity index (c) at the end of the greenhouse experiment. Letters indicate differences between main effects of moisture and arrival treatments (Bonferroni, $P < 0.05$).

than when sown first (Fig. 4g, Table 1). FMP seedling turnover was positive, but not affected by arrival order or soil moisture (Fig. 4h, Table 1).

The increase in total seedling numbers per treatment over time strongly differed between wet and dry plots, and we observed significant interactions between time and moisture (Fig. 5; repeated measures LMM $F_{2,48} = 10.3$, $P < 0.001$), as the increase in total seedling numbers in wet plots was steeper compared to dry plots. Further, we found an interaction between time and arrival order (repeated measures LMM $F_{4,47} = 4.1$, $P = 0.007$) as the seedling numbers in the FMP first treatment decreased after winter. We also observed a trend between arrival order and moisture (repeated measures LMM $F_{2,49} = 2.8$, $P = 0.07$) as seedling numbers in the BS first treatment tended to be higher compared to the control under wet conditions but not under dry conditions. The overall effect of arrival order and soil moisture, and the three-way interaction (arrival order \times soil moisture \times time) were not significant. We measured more variable soil moisture conditions in wet treatment blocks than in dry blocks (independent t -test on moisture over time $df = 47$, $P = 0.003$). Because of the interaction between time and soil moisture, we tested the temporal patterns for each of

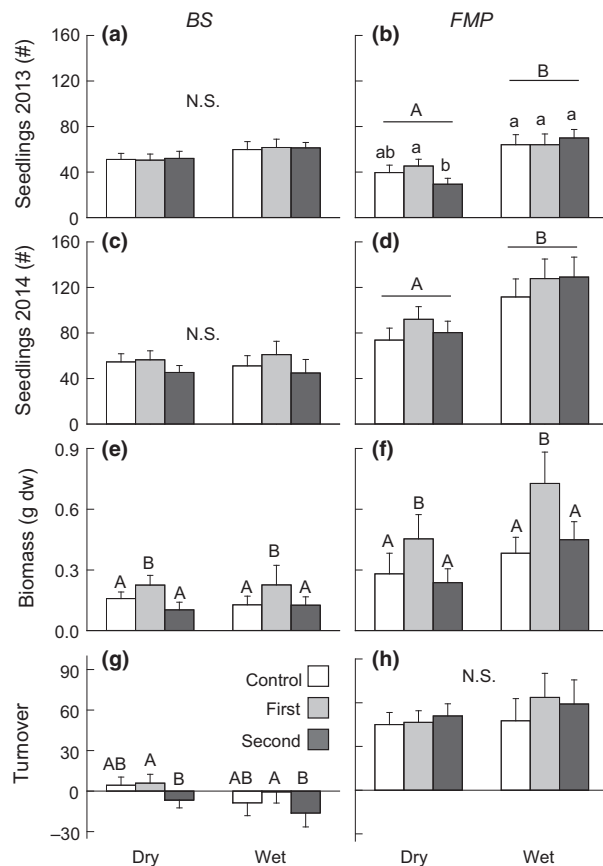


Fig. 4. Effects of arrival order and soil moisture treatments on seedling numbers in Aug 2013 and 2014 (a d), harvested biomass (e f), and seedling turnover from Aug 2013 to Aug 2014 (g, h) for BS (a, c, g, e) and FMP (b, d, f, h) seedling groups in the field experiment. Uppercase letters indicate differences between main effects of moisture and arrival order treatments and lowercase letters indicate differences within moisture treatments (Bonferroni, $P < 0.05$).

the two moisture classes separately. The total seedling numbers increased over time under dry conditions (LMM, time $F_{2,30} = 14.1$, $P < 0.001$; Fig. 5a), with significantly higher numbers in Aug 2013 compared to 2014. However, seedling number was unaffected by arrival order (LMM, arrival order $F_{2,31} = 0.27$, $P = 0.768$). In contrast, under wet conditions the total number of seedlings decreased after the winter, with the decrease depending on arrival order (LMM, interaction effect $F_{4,18} = 3.41$, $P = 0.031$): the decrease was strongest in FMP first treatments and weakest in BS first treatments ($P < 0.05$ Bonferroni post-hoc test) (Fig. 5b). During the summer of 2014, seedling numbers increased again, and after two growing seasons the total number of seedlings was not affected by arrival order or soil moisture (Fig. 5b, Table 1).

Total standing biomass was significantly affected by arrival order (Table 1). It was higher in the FMP first treatment compared to the control, but the BS first treatment did not

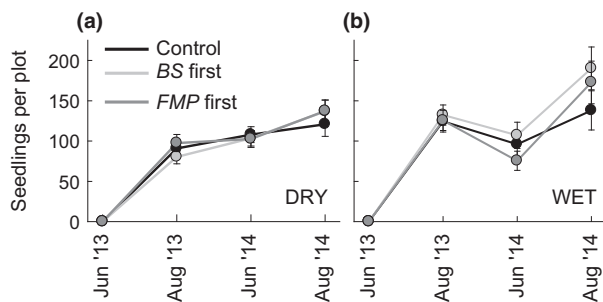


Fig. 5. Effects of arrival order (simultaneous arrival (Control), BS first and FMP first) on total number of seedlings over time in dry (a) and wet plots (b). Data are means \pm SE.

differ from the other treatments. The Shannon diversity index was not affected by arrival order but was lower in dry than in wet plots in 2013. However, in 2014, the difference between dry and wet plots was only marginally significant (Table 1, Appendix S5).

Strength of priority effects

In both the field and greenhouse experiments, priority effects were generally stronger for species with low relative abundance (Fig. 6a,c). Changing soil moisture induced shifts in both the relative abundance and the strength of priority effects, which was also observed in the RGR of the greenhouse plants (Fig. 6b). *Solidago*, the species with the driest habitat preference, had higher abundance and weaker priority effects in the dry compared to the wet treatment blocks. The other species, with preference for wetter habitats, showed opposite responses, but there was no correlation between habitat moisture value and priority strength in the field experiment (Fig. 6c,d). In the field, the species-specific shifts in relative abundance and priority strength resulted in a significant correlation between relative abundance and strength of priority effects under dry conditions (Pearson $r = 0.896$, $P = 0.04$), but not under wet conditions (Pearson $r = 0.664$, $P = 0.222$; Fig. 6c). For the greenhouse experiment, we did not have enough data to statistically test for correlations per treatment.

Discussion

Priority effects

In line with our first hypothesis, we found strong priority effects on plant performance both in the greenhouse and in the field, with the priority effects on plant biomass being persistent over two growing seasons in the field and with consistent patterns within most individual species. We also found priority effects on plant community diversity, and those effects were stronger in the laboratory than in the

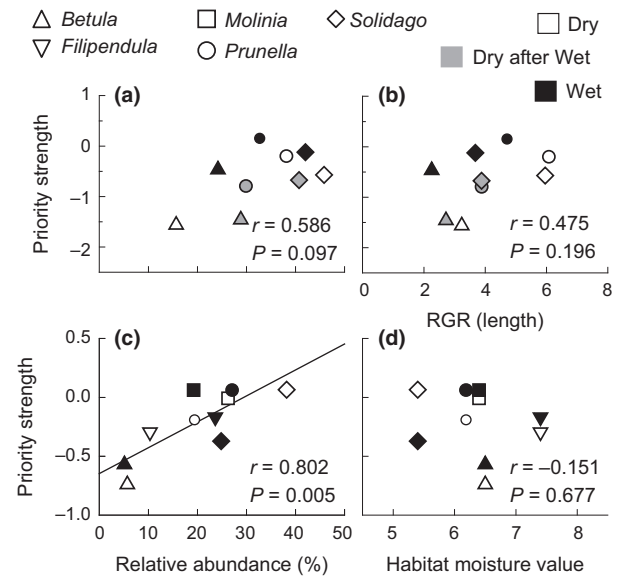


Fig. 6. Relationship between species performance measured as (a, c) relative seedling abundance when all species were sown simultaneously, (b) RGR and (d) habitat moisture value and the strength of priority effects for the different species in (a, b) the greenhouse and (c, d) the field experiment.

field. In both cases, we observed lower diversity in treatments with phased arrival. The few tests of priority effects under field conditions often report a lower diversity in phased arrival treatments and sustained divergence of plant community composition after 1, 3 and 5 yr (Eriksson 1997; Ejrnæs et al. 2006; Martin & Wilsey 2014; Vaughn & Young 2015). These studies mostly used 1-yr sowing intervals, except for Vaughn & Young (2015), who showed priority effects at 2-wk sowing intervals. Our study also shows that small differences in arrival time, which are more realistic and relevant under natural conditions (Boedeltje et al. 2004; Pakeman & Small 2005; Sarneel et al. 2014), can affect plant community assembly and diversity. Some indirect observations provide further evidence for priority effects in naturally assembled communities. For example, tree rings of *Populus fremontii* in a floodplain forest showed that most trees had established shortly after a management shift (Stella et al. 2011). We therefore conclude that also in riparian ecosystems, priority effects can determine plant species community assembly, at least at local scales, and therefore are important to consider in (riparian) ecosystem management (Lulow 2006; Pluckers et al. 2013) or when addressing effects of climate change that interact with timing of dispersal.

Interactions with soil moisture

We observed that higher soil moisture favoured plant performance of most species as it increased germination and

also seedling biomass, which was significant in the greenhouse and for the *FMP* species group also in the field experiment. With regard to our second hypothesis, soil moisture interacted with arrival order, decreasing seedling numbers for late-arriving species in the dry and dry-after-wet treatment (or both), but not in the wet treatments. This was observed for both species groups in the greenhouse and for *FMP* in the field. These results therefore challenge the general assumption that priority effects mainly occur under benign conditions where species arriving first benefit most from the available resource (Chase 2003; Kardol et al. 2013; Tucker & Fukami 2014; Vannette & Fukami 2014). Our results are more in line with Clements et al. (2013) who observed the strongest effects of arrival order on ciliate communities at either warm or cold temperatures compared to more favourable intermediate conditions. We currently lack good explanations for such patterns. In our study, we found indications that species-specific reactions to soil moisture may have played a role. Wet conditions negatively affected the performance of the most drought-tolerant species (*Solidago*), which in turn increased the strength of priority effects, whereas opposite patterns were found for species adapted to wetter conditions. Priority effects may be better understood when assessing species performance, resource use or niche overlap rather than from a general assessment of the habitat conditions or resource availability *per se*, although those can be related (Chase 2003; Ejrnæs et al. 2006; Vannette & Fukami 2014).

It has been hypothesized that resource variability decreases the importance of priority effects by reducing the competitive advantage of the species arriving first (Tucker & Fukami 2014). As experiments with variable environmental conditions (such as our dry-after-wet treatment) are scarce, the importance of resource variability in attenuating priority effects is still poorly understood. In the field, wet plots were more variable in soil moisture than dry plots. Yet we observed stronger priority effects on community seedling numbers in wet compared to dry treatment plots, with differences appearing after winter and the subsequent spring flood. This indicates that wet plots likely faced a higher flooding disturbance, which induced high mortality of species arriving second, especially for *Solidago* that favours dry habitats. *Solidago* seedlings arriving second may have been more vulnerable to flooding stress compared to the other species better adapted to wet conditions, and compared to *Solidago* seedlings that arrived 3 wk earlier. These findings indicate that resource availability and habitat variability should not be considered in a general sense; instead, species-specific patterns of resource use may be more informative in explaining priority effects in plant community assembly (Fukami et al. 2005; Vannette & Fukami 2014).

Strength of priority effects

We consistently observed that species with a high performance in the control treatments were less prone to priority effects, which supports our third hypothesis. Furthermore, when habitat conditions favoured species performance in the field, the importance of priority tended to decrease. This is in line with the body size-dependent priority effects observed for dragonfly nymphs (Rasmussen et al. 2014). For plants, theory predicts that under strong competitive pressure, the order of species arrival is of minor importance as the most competitive species, sooner or later, will become dominant regardless of history (Fukami 2015). Yet we show that even though arrival order may be unimportant for the dominance of the most competitive or best-performing species, and thereby on community biomass, the presence and relative abundance of less-competitive species will depend on arrival order. As such, priority effects may help to maintain subordinate species that can exert disproportional effects on ecosystem functions and increase resilience of vegetation to environmental fluctuations (Mariotte et al. 2013).

Species performance may also depend on traits other than size. In particular, functional traits that determine flooding resistance, nutrient acquisition or recruitment may exert strong priority effects. For instance, Körner et al. (2008) and von Gillhausen et al. (2014) observed that when legumes arrived first, communities remained more similar to the control where species groups arrived simultaneously compared to communities where forbs or grasses arrived first. In our study, RGR (related to competitive strength) and plant performance (integrating seed viability and plant competition) showed the same positive relation with strength of priority effects but the relationship was less strong for RGR. This indicates that besides growth, differential germination may contribute to priority effects and that the role of other traits and different life stages should be addressed to understand the importance of the interaction between habitat and arrival order.

Perspectives for the riparian ecosystem

We found that priority effects determine species occurrence and can affect plant species composition under controlled greenhouse conditions as well as under field conditions. Higher soil moisture reduced the importance of priority effects for most tested riparian species. This suggests that riparian vegetation composition is influenced by the timing of different seed fluxes. In boreal zones, seeds from the seed bank would be the first to germinate after snow melt. Those seeds may have a competitive advantage over seeds arriving later via floods or other means of dispersal. In this way, priority effects may partly explain the

often-observed weak correlation between seed deposition through floods and the numbers of recruiting seedlings (Andersson et al. 2000; Sarneel et al. 2014).

Personal observations showed that natural seedling numbers in boreal riparian vegetation are generally low (around 10 m⁻²). Seedling densities such as those observed in our study, however, are found locally on recently disturbed places, e.g. when trees have fallen into the river or when sediment has been deposited during floods. These patches of bare soil are often close to the river where flood-deposited seeds are the first to arrive, when the soil is still relatively moist compared to later in the season. As such, seeds that arrive later by other means of dispersal may have a lower probability of establishment after disturbance. This may help to explain the dominance of plant species with highly buoyant seeds in riparian zones. It may also explain the shift from dominance of wind-dispersed species to water-dispersed species with increasing stream order and thereby increasing disturbance (Kuglerová et al. 2015). Although our experiment represented realistic field conditions, the importance of priority at wider spatio-temporal scales requires further research. Taken together, our study indicates that when flooding and disturbance regimes change, for instance due to climate change, hydropower management or ecological restoration (Ström et al. 2012), taking into account the interactions between arrival order, species identity and habitat conditions, would advance our understanding and predictive competence of vegetation changes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species characteristics.

Appendix S2. Location details.

Appendix S3. Germination in the control quadrats of the field experiment.

Appendix S4. Statistical details.

Appendix S5. Community-level differences in the field.

Appendix S6. Table described in Appendix S1.

Appendix S7. Table described in Appendix S2.

Appendix S8. Table described in Appendix S3.

Appendix S9. Tables described in Appendix S4.