Received: 4 October 2016 | Revised: 12 February 2017 | Accepted: 13 February 2017

DOI: 10.1111/gcb.13687

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Effects of increased flooding on riparian vegetation: Field experiments simulating climate change along five European lowland streams

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Funding information
EU 7th Framework Project REFRESH, Grant/Award Number: 244121; AstroTurf®

Abstract

In many parts of the world, the magnitude and frequency of cold-season precipitation are expected to increase in the near future. This will result in an increased magnitude and duration of winter and spring flooding by rain-fed streams and rivers. Such climate-driven increases in flooding are likely to affect riparian plant communities, but future vegetation changes are hard to predict due to current lack of data. To fill this knowledge gap, we experimentally modified the hydrology of five streams across three countries in north-western Europe during late winter/early spring over a period of 3 years. We assessed the responses in riparian plant species richness, biomass, plant-available nitrogen and phosphorus and seed deposition to increased flooding depth (+18 cm on average at the lowest positions along the riparian gradient) and prolonged flooding duration (6 weeks on average). After 3 years of increased flooding, there was an overall decline in riparian species richness, while riparian plant biomass increased. Extractable soil nitrogen and phosphorus also increased and are likely to have contributed to the increased biomass. Increased flooding resulted in the arrival of more seeds of additional species to the riparian zone, thereby potentially facilitating the shifts in riparian plant species composition we observed. The results of our concerted experimental effort demonstrate that changes in stream riparian plant communities can occur rapidly following increased winter flooding, leading to strong reductions in plant species diversity.

KEYWORDS

biodiversity, floods, global change, hydrological changes, nutrient availability, plant species composition, riparian zone, seed deposition, stream riparian gradient, wetlands

1 | INTRODUCTION

The magnitude and frequency of intense precipitation events are expected to increase in many parts of the world in the near future (Bates, Kundzewicz, Wu, & Palutikof, 2008; IPCC, 2007), and, consequently, risks of stream and river flooding are projected to rise (Dankers & Feyen, 2009; Hirabayashi et al., 2013). This will impact streams, rivers and their terrestrial surroundings, as major effects on the nutrient and sediment dynamics of the flooded areas can be anticipated with possibly drastic consequences for vegetation and fauna (Naiman & Décamps, 1997; Poff et al., 1997; Merritt, Scott, Le Roy Poff, Auble, & Lytle, 2010).

Stream riparian zones are ecotones that constitute the transitional area between aquatic and terrestrial ecosystems. The riparian zone starts at the stream and extends across the floodplain, including the whole area that is influenced by the waterway (Gregory, Swanson, McKee, & Cummins, 1991; Naiman & Décamps, 1997; Naiman, Décamps, & McClain, 2005; Verry, Dolloff, & Manning, 2004). Riparian ecosystems are of great ecological importance because they are characterized by high biodiversity and provide several important ecosystem services, including the storage and purification of water and the provisioning of spawning habitat for fish (Capon et al., 2013; Naiman & Décamps, 1997; Naiman, Décamps, & Pollock, 1993; Richardson et al., 2007; Verhoeven, Arheimer, Yin, & Hefting, 2006). Their high plant diversity is caused by strong environmental gradients (Naiman et al., 1993): Riparian plant communities are structured across the riparian zone according to differences in the specific niches of the species, based on hydrology and soil properties (Fraaije, ter Braak, Verduyn, Breeman, et al., 2015; Silvertown, Dodd, Gowing, & Mountford, 1999; Ström, Jansson, Nilsson, Johansson, & Xiong, 2011) and on the differential arrival of plant seeds with rising and falling water levels (Fraaije, ter Braak, Verduyn, Verhoeven, & Soons, 2015; Soons et al., 2016). Particularly, strong species sorting occurs at the lower elevations close to the stream, where seed arrival, plant establishment and survival are determined by flooding (Fraaije, ter Braak, Verduyn, Breeman, et al., 2015; Fraaije, ter Braak, Verduyn, Verhoeven, et al., 2015; Lenssen & de Kroon, 2005; Silvertown et al., 1999).

Riparian ecosystems along lowland streams are often regarded as vulnerable to climate change due to their sensitivity to changes in precipitation (Catford et al., 2013; Décamps, 1993), resulting in changes in their hydrology and, subsequently, their vegetation (Garssen, Baattrup-Pedersen, Voesenek, Verhoeven, & Soons, 2015; Garssen, Soons, & Verhoeven, 2014). Considering flooding, the timing, frequency, magnitude (water depth) and duration of inundation are all critical for the arrival, establishment and survival of plant species (Fraaije, ter Braak, Verduyn, Breeman, et al., 2015; Fraaije, ter Braak, Verduyn, Verhoeven, et al., 2015; Garssen et al., 2015; Van Eck, Lenssen, Rengelink, Blom, & de Kroon, 2005; Van Eck, van de Steeg, Blom, & de Kroon, 2004; Voesenek, Rijnders, Peeters, van de Steeg, & de Kroon, 2004). Seed transport by water is an important dispersal mechanism in riparian zones (Moggridge & Gurnell, 2010; Moggridge, Gurnell, & Mountford, 2009), which contributes to species sorting along the hydrological gradient (Fraaije, ter Braak, Verduyn, Verhoeven, et al., 2015; Soons et al., 2016). Mechanisms of plants to subsequently germinate and tolerate flooding are largely species specific and further define their distribution along the riparian gradient (Chen, Qualls, & Miller, 2002; Fraaije, ter Braak, Verduyn, Breeman, et al., 2015; Fraaije, ter Braak, Verduyn, Verhoeven, et al., 2015; Garssen et al., 2015; Lenssen & de Kroon, 2005; Visser, Colmer, Blom, & Voesenek, 2000; Voesenek et al., 2004). Additionally, riparian plant communities may be affected by increased sedimentation during flooding events, which often results in large inputs of nitrogen (N) and phosphorus (P) into the riparian system (Craft & Casey, 2000; Kronvang, Hoffmann, & Dröge, 2009; Noe, Hupp, & Rybicky, 2013). More indirectly, inundation influences biogeochemical processes that control nutrient availability (Olde Venterink et al., 2006) through depletion of oxygen in upper soil layers (Beumer, van Wirdum, Beltman, Griffioen, & Verhoeven, 2007; Drew, 1997; Mitsch & Gosselink, 1993). In anoxic environments rich in organic matter, denitrification may decrease N availability (Hefting, 2003), while phosphate mobilization may increase P availability ("internal eutrophication"; Roelofs, 1991; Mitsch & Gosselink, 1993; Smolders & Roelofs, 1993; Smolders, Lucassen, Bobbink, Roelofs, & Lamers, 2010). Finally, strongly reduced conditions may also lead to a build-up of phytotoxin levels in the soil, such as sulphide, a harmful substance for riparian plant species (Lamers, Tomassen, & Roelofs, 1998; Smolders, Lamers, Den Hartog, & Roelofs, 2003).

Species shifts following flooding may thus lead to increased or decreased riparian species richness, depending on the nutrient availability and climatic and hydrological status of the catchment (Garssen et al., 2015). While laboratory and glasshouse experiments have examined the effects of flooding on the performance of selected plant species at specific growth stages (Garssen et al., 2015), ecosystem responses are complicated and cannot simply be derived from summing the responses of individual species determined under laboratory and glasshouse conditions. Only very few studies have investigated flooding effects at the ecosystem level experimentally, for example focusing on flooding effects on exotic species using natural experiments (Greet, Webb, & Cousens, 2015; Lunt, Jansen, & Binns, 2012). These studies showed that flooding resulted in an decrease in exotic plant species already after 1 year of flooding. It was our aim to investigate empirically the effects of increased flooding duration and water depth on entire riparian plant communities and soils under natural conditions. For this purpose, we carried out a series of field experiments that actively manipulated stream water discharge and associated flooding events. Such experiments have rarely been performed in the past, due to the major effort and costs involved as well as difficulties in obtaining approval by water boards and potential stakeholder conflicts (Ström et al., 2011).

Our study took advantage of a unique European research network (EU-funded FP7 project REFRESH) to run a three-year field experiment in five European lowland streams (Figure 1). We conducted this field experiment to specifically investigate the following: (1) the overall responses in riparian plant species richness, composition, biomass, seed arrival and plant-available N and P to increased flooding duration and water depth, (2) the environmental variables that correlate with changes in species composition, and (3) the extent to which seed deposition results in the arrival of new species and contributes to species turnover.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

Five riparian areas in Denmark, Germany and the Netherlands were selected for the flooding experiment (Figure 1a). In Denmark, the riparian areas were situated along a channelized agricultural stream (Voel bæk, Figure 1b) and a more pristine forest stream (Sandemandsbækken, Figure 1c). These riparian zones were formerly used as grazing land for horses and cattle. In Germany, the riparian area was

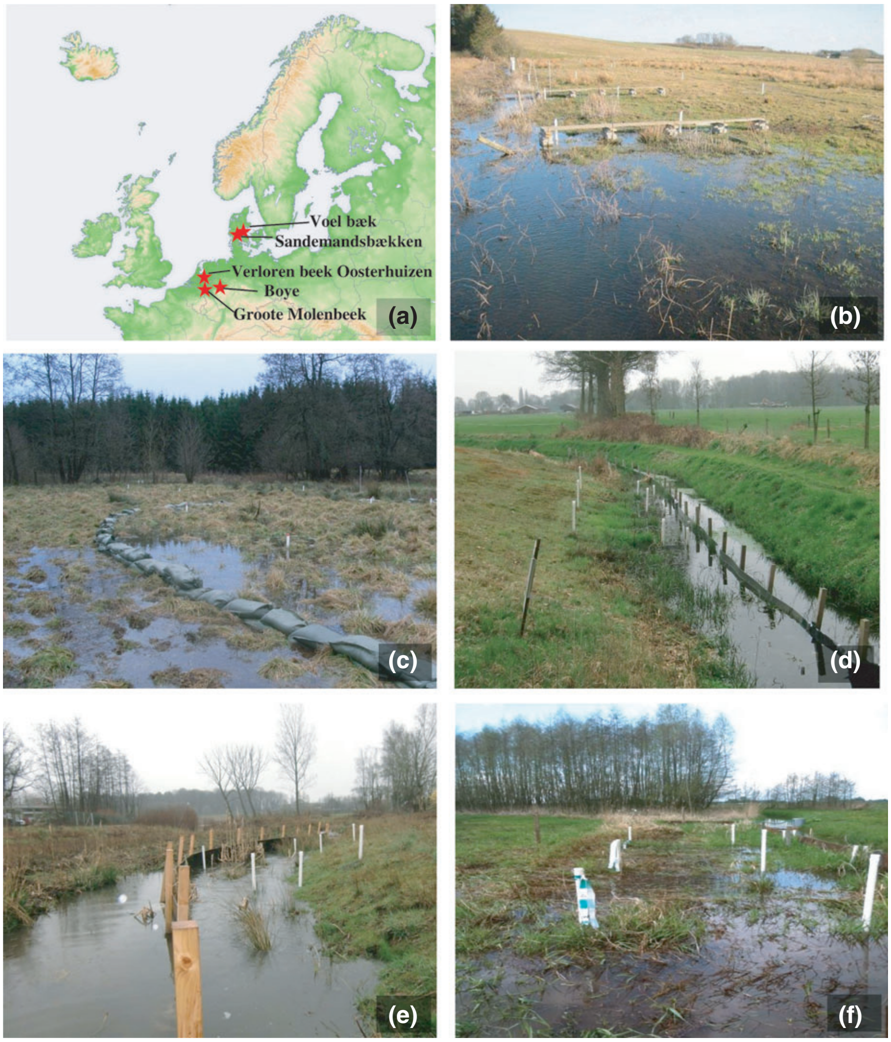

FIGURE 1 Overview of the locations of the stream riparian wetland sites in north-western Europe (a), with pictures of the flooding treatments: Voel bæk (Denmark) (b), Sandemandsbækken (Denmark) (c), Verloren beek Oosterhuizen (the Netherlands) (d), Boye (Germany) (e), Groote Molenbeek (the Netherlands) (f). [Colour figure can be viewed at wileyonlinelibrary.com]

located along the head reach of a restored stream (Boye, Figure 1e) which had not been managed or cultivated recently. In the Netherlands, the riparian areas were situated along agricultural streams of which the riparian zone has been partly restored (Verloren beek Oosterhuizen, Figure 1d; Groote Molenbeek, Figure 1f). At the latter two sites, in-stream vegetation was mown twice a year, while the riparian vegetation was mown once a year (at the end of the growing season). More details on all streams are given in Table 1.

The experimental areas were laid out in the riparian zones stretching over a length of approximately 100–150 m along each stream, and control and flooding-treatment sections with similar plant communities were selected. We positioned a dam construction in each flooding-treatment section to create a significantly higher surface water level than under normal winter conditions (see Appendix S1). In the control sections, stream water levels were not manipulated. The flooding experiments were conducted during three consecutive years (2011–2013). The manipulated flooding extended the normal winter flooding by 6–8 weeks each year in the period from March to mid-April and increased inundation water depth at the lowest sampling points from an average of 0.08 m to an average of 0.29 m compared to the water depths in the plots that were not manipulated (Table 2). In 2013, the flooding experiment in Denmark commenced at the end of April and ended mid-June, because frozen soil prevented earlier manipulations. During the flooding experiments, floods occurred as a result of relatively stable flow velocities (data not shown).

Within each section, three transects perpendicular to the stream were selected along the stream riparian gradient, ranging from the lowest water level of the stream under summer base flow conditions to the highest point up the stream valley that can be flooded by surface water during extreme winter floods. Measurements were carried out at three sampling points (short belt transects that ran along the experimental or control reaches at appropriate elevation, to allow sufficient space for all measurements specified below) along each transect (Figure 2), so that there were nine samples for each variable per stream section and 90 samples in total (nine samples $\times$ two sections $\times$ five streams). Selection of the locations was based on records of recent water levels and expert judgement. The first sampling points were situated closest to the stream, just above the normal summer water level. These points are normally not inundated in summer, but inundated during winter floods. Our flooding treatment prolonged the duration of winter flooding at

TABLE 1 Name, location, climate characteristics, catchment size and date of restoration activities of the stream riparian wetland sites used for the flooding experiments

Name	Country	Coordinates in lat/long	Average winter–summer temperature in °C	Average winter–summer precipitation in mm/month	Catchment area (ha)	Restoration (year)
Voel bæk	DK	56°19′58.46″ N 9°70′39.32″ E	0.88–15.56 (N = 15)	20.67–28.39 (N = 15)	757.5	Not restored
Sandemandsbækken	DK	56°15′85.07″ N 9°49′61.20″ E	2.01–15.49 (N = 15)	21.64–28.86 (N = 15)	7.1	2003[a]
Boye	DE	51°58′61.13″N 6°91′10.01″E	2.58–18.05 (N = 15)	62.68–90.16 (N = 15)	340	2002[b]
Verloren beek Oosterhuizen	NL	52°15′91.13″N 6°02′11.54″E	2.55–16.94 (N = 450)	71.38–98.90 (N = 450)	1,208	2005[c]
Groote Molenbeek	NL	51°39′17.32″N 6°03′59.47″E	2.73–17.74 (N = 450)	61.15–82.90 (N = 450)	18,356	2000[d]

[a]Restoration activities included remeandering of the streambed, restoring the stream's natural dimensions.
[b]Restoration activities included flattening of both riparian gradients, broadening of streambed.
[c]Restoration activities included flattening of northern riparian gradient.
[d]Restoration activities included remeandering of the streambed.

TABLE 2 Average differences in water level (either surface water (positive values) or groundwater (negative values), measured by a sounding device) in cm across all sampling points in the flooding sections and control sections at the five streams. Data are displayed for the final year, 2013

Stream name	Sampling points 1	Sampling points 2	Sampling points 3
Voel bæk (DK)	+8	+10[a]	+1
Sandemandsbækken (DK)	+10	+22[a]	+11
Boye (DE)	+29	+15	−8
Verloren beek Oosterhuizen (NL)	+24	+16	−9
Groote Molenbeek (NL)	+20	+8	+5

[a]Due to topographic differences, this average increase in water levels was higher compared to the first sampling point.

these points and increased the depth of inundation. The second sampling points were situated just above the normal winter water level, so that they are normally not flooded in summer or winter. Our flooding treatment resulted in inundation of these points during the experimental period in late winter/early spring. The third sampling points were situated at the high end of the floodplain, flooded only during rare extreme winter floods (approximately every 100 years). These points were never inundated, but our flooding treatment generally resulted in higher groundwater levels during the treatment period. The second series of sampling points was expected to be most affected by the flooding treatment in comparison with the control situation.

2.2 | Measurements

During each manipulated flooding period (6–8 weeks), in-stream water levels were continuously monitored in piezometers with a screen over the complete buried length, using a Diver®; manual measurements using a sounding device were carried out in similar piezometers at all sampling points at the start of the experiment, after the second and fourth week and at the final stage of the experiment. Samples of groundwater/surface water and soil pore water were collected on a biweekly basis at each sampling point during the experiment. Samples of stream surface water were taken from the middle part of each stream. Rhizons (Rhizosphere®) were used to collect soil pore water. The water was inserted into bottles immediately, stored at 4°C and filtered over Whatman® glass microfibre filters (type GF/C) before analysis. Ammonium, total N and total P in the water samples were measured according to European standard methods (EN ISO 11732; EN ISO 13395; EN ISO 6878, respectively). Each year, after the end of the flooding treatment (April/May), potential plant-available nutrients were determined for a pooled sample from three soil cores of the top 10 cm of soil surrounding each sampling point. In the laboratory, the pooled samples were extracted with 0.4 M potassium chloride to assess extractable soil N; nitrate and ammonium in the extracts were measured on an auto-analyser (Skalar Continuous Flow Analyser (CFA) and Lachat QC-8000 Flow Injection Autoanalyzer (Lachat Instruments, Loveland, CO, USA). Extractions with 0.5 M sodium carbonate were carried out to determine extractable soil P (Olsen, Cole, Watanabe, & Dean, 1954).

In the summers following the manipulated flooding periods, plant aboveground biomass at the sampling points was clipped at a 50×50 cm^2 plot at peak standing crop (August), oven-dried (48 hr, 70°C) and weighed. Vegetation relevés were made in another, nonharvested 50×50 cm^2 permanent plot near each sampling point during the growing season (June–September). Species composition was recorded according to the Braun-Blanquet method (1928), adjusted by Barkman, Doing, and Segal (1964). Percentage coverage was estimated for all vascular plant species. Data were converted to Ord% scale (coverage ranges from 0.5 to 140), according to van der Maarel (2007), to be able to conduct ordinations. Species turnover was calculated for each individual plot, computing species gains, losses and number of equal species within the experimental period (2011–2013). Relative species turnover rates were calculated using the following equation: 100 × (species loss + species gain)/(species loss + species gain + equal species; Peterson et al., 2002).

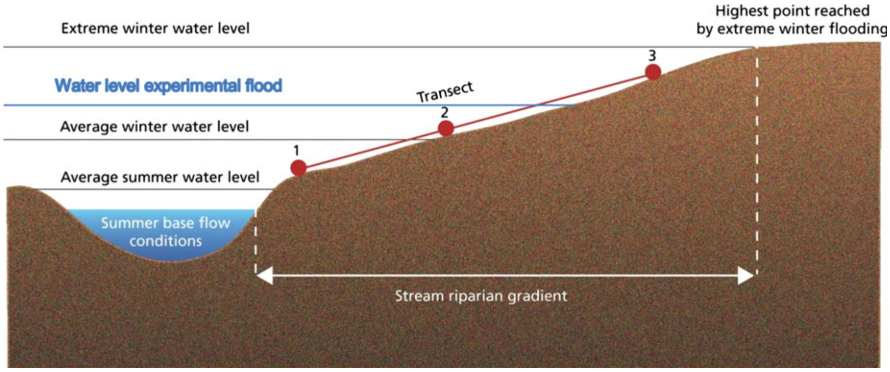

FIGURE 2 Schematic cross section of the stream riparian gradient and location of sampling points (1 (low), 2 (middle) and 3 (high)) in relation to average water levels. [Colour figure can be viewed at wileyonlinelibrary.com]

Seed traps consisting of 25 × 22.5 cm artificial grass mats with plastic bristles (Astroturf®) were secured along the riparian gradient close to each sampling point (one trap per sampling point) to quantify sediment and seed deposition during the period of the manipulated flooding treatment (cf. Goodson, Gurnell, Angold, & Morrissey, 2003) at the Voel bæk, Sandemandsbækken, Boye and Groote Molenbeek in the year 2011–2012. In the laboratory, the deposited material was oven-dried (48 hr, 70°C,) and weighed to determine the amount of sediment deposited. Seeds were hand-picked from the sediment samples (following Fraaije, ter Braak, Verduyn, Verhoeven, et al., 2015) and identified to species level using the "Digital Seed Atlas of the Netherlands" (Cappers, Bekker, & Jans, 2006).

2.3 | Data analysis

The overall responses to increased flooding depth for riparian plant species richness, biomass, plant-available N and P and seed deposition were examined by regression analysis and using a set of linear mixed models (LMMs, type I sum of squares). We here present the results for the data collected from the final experimental year (2013), as these represent the most long-term effects, except for the seed deposition data which were collected only in the first year (2011). We used the simple regression analysis to present the direct relation between the response variables and water table. Using the LMMs, we were able to identify the relations between the response variables, treatments and other potential explaining variables in detail. In the LMMs, stream was defined as a random factor, with section built in as a nested term. As the level of inundation achieved by the experimental design varied between sampling points and sites, the average water level during the manipulated flooding period was included as a covariate in the models. The flooding-treatment effect was examined by analysing section and the interaction between section and water level as the main (and last added) factors in the model. We further examined the changes in environmental variables that correlate with alterations in the response variables by consecutively including average annual temperature, extractable soil N, extractable soil P, groundwater N, groundwater P and plant biomass as covariates in the model. Additionally, we tested for relevant correlations using bivariate correlations and calculating Pearson correlation coefficients. The above tests were all performed using IBM SPSS Statistics version 20.

We summarized the variation in riparian plant species composition using unconstrained correspondence analysis (CA). In this CA, the plant determination data were entered and the summary was interpreted with the help of environmental variables (latitude, temperature, water level, biomass, N concentration in surface water and groundwater, P concentration in surface water and groundwater, extractable soil N and P). To visualize the effects of the flooding treatment and the position of the sampling points on species composition along the riparian gradient, we conducted CAs for each stream separately and demarcated the three positions of sampling points along the gradient with plot envelopes. Finally, we examined the similarity between seed and adult plant species composition along the stream riparian gradient for each stream, again using CAs. In all CAs, we log-transformed response data (species composition) and downweighted rare species to obtain normal distributions. All CAs were performed using CANOCO version 5.0 (Ter Braak & Šmilauer, 2012).

3 | RESULTS

The flooding treatment was successfully applied for an average of 6 weeks each year. At the Danish streams, the difference in water levels between the control and flooding sections was less noticeable compared to the Dutch and German streams, especially at the first sampling points along the riparian gradients (Table 2). At the third sampling points along the riparian gradients, the Verloren beek Oosterhuizen and Boye sites showed an opposite difference in water level between the control and flooding sections. This was mainly due to a steeper riparian gradient at the flooding sections at these sites, compared to the control sections.

3.1 | Riparian plant species richness

Pronounced negative responses of riparian species richness to increased winter flooding were generally detected along all streams after 3 years of manipulation. In 2013, species richness averaged 8.7 and 5.9 species per plot for the flooding-treatment and control sections, respectively (Appendix S2). Relative species turnover rates in the flooding section plots were higher compared to the control section plots (75% vs. 61% of the total number of species;

Appendix S2). At the flooding sections, species richness and water level were significantly negatively related (p = .003), while no such relation was found for the control sections (p = .536; Figure 3a). LMM revealed a general negative (cor)relation between species richness and water level and a (almost significant) positive interaction between section and water level, which indicates that the negative effect of the flooding treatment was more pronounced at the lower plots (higher water levels; Table 3). Additionally, plant species richness was negatively related to total plant biomass and plant-available N (Table 3, Appendix S3).

3.2 | Riparian plant biomass

In contrast to what was observed for species richness, a strong positive relation between plant biomass and water level was detected for the flooding sections (p = .002), while no such relationship was found for the control sections (p = .558; Figure 3b). No general relation between biomass and water level was observed, but the interaction between section and water level was significantly negative (Table 3), supporting the observation that there was only a positive relation between biomass and water level at the flooding sections.

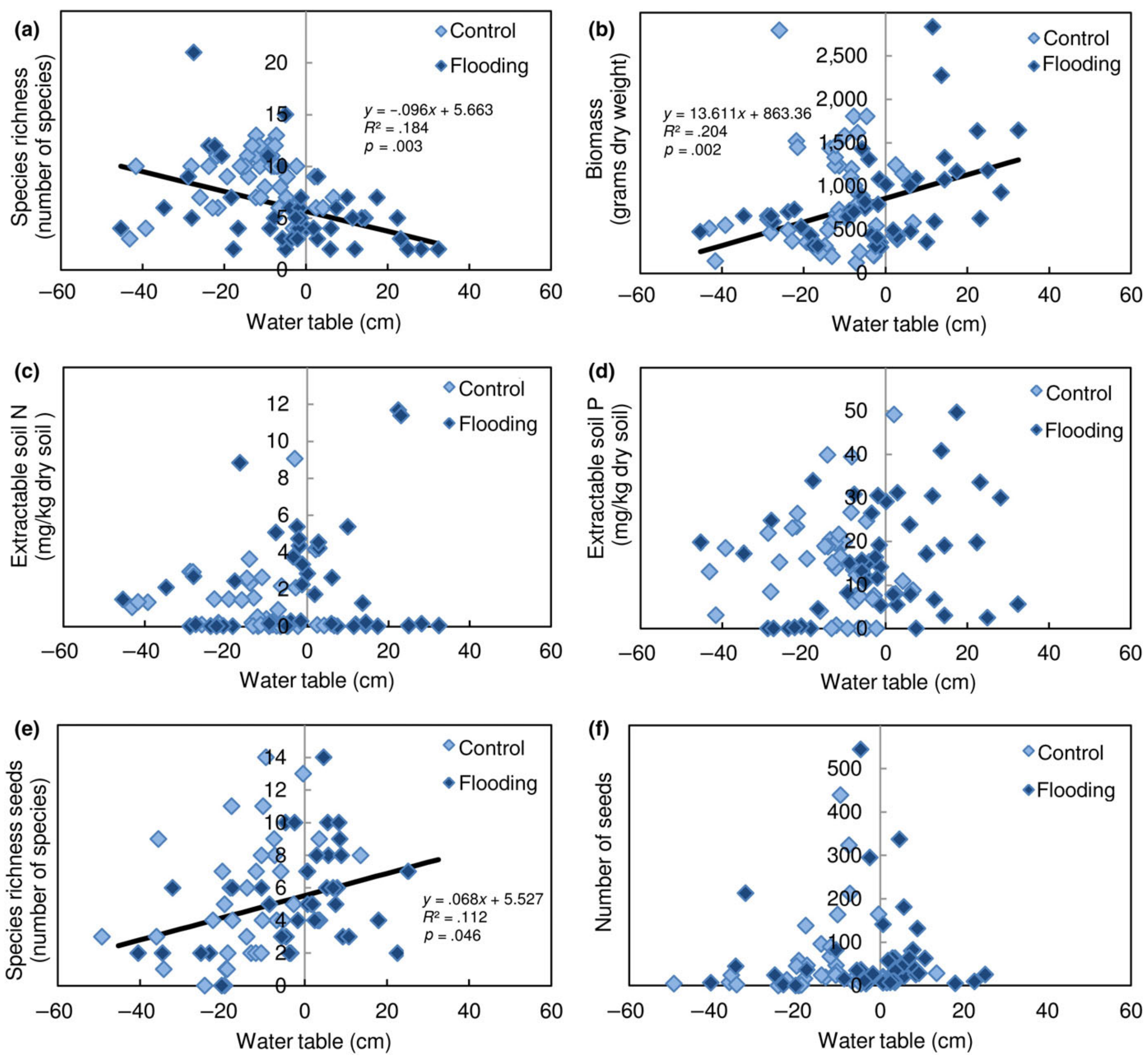

FIGURE 3 Vegetation and soil characteristics in relation to water level in control and flooded plots along the five investigated European lowland streams: Species richness of the riparian vegetation (a), aboveground plant biomass (b), extractable soil N (c), extractable soil P (d), species richness of deposited seeds (e) and numbers of deposited seeds (f). Data points represent data per sampling point for the final year of the experiments (2013). A positive water level indicates that the sampling point was inundated during the manipulated inundation period in late winter. N = 45 for the control sections, N = 45 for the flooding sections, except for deposited seeds (e and f), where N = 36 for both. Regression statistics for significant relations within flooding or control sections are displayed in the graphs. [Colour figure can be viewed at wileyonlinelibrary.com]

Furthermore, biomass was also strongly positively related to site temperature and soil extractable P (Table 3, Appendix S3).

3.3 | Extractable soil N and P

The linear relationship between extractable soil N and water level was nearly significant for the flooding sections (p = .074), and the control sections showed no evidence of such a relationship (p = .809; Figure 3c). Patterns related to extractable soil P and water levels were less clear (Figure 3d). In the LMM, however, extractable soil N and P were both positively related to water level (Table 3, Appendix S3), indicating that extractable soil N and P increased following the late winter flooding treatment.

3.4 | Seed and sediment deposition

In contrast to vegetation species richness, a positive relation was found between species richness of deposited seeds and water level, both at the flooding and control sections (p = .046, p = .051; Figure 3e; Table 3, Appendix S3). The species richness of deposited seeds was also positively related to the number of deposited seeds (p < .001 in the LMM, Appendix S3). No linear relation was found between the number of deposited seeds and any other variables, with the exception of temperature (Table 3, Appendix S3). The number of deposited seeds showed a clear optimum around the waterline (water levels close to zero; Figure 3f), and this nonlinear relation likely explains the lack of correlation with water level in the LMM.

Species richness of deposited seeds was strongly positively correlated with total number of deposited seeds and with sediment deposition (p < .001, Pearson's correlation coefficient of 0.737 and 0.606, respectively). Sediment deposition was also strongly positively correlated with extractable soil N (Pearson's correlation coefficient r = .828, p < .001), while there was no significant correlation with extractable soil P (p = .132).

3.5 | Riparian plant species composition and environmental variables

Riparian plant species composition along the five European lowland streams is plotted for the final experimental year 2013 (Figure 4). The percentage of variance in species abundances explained by the first ordination axis was 9.11, and by the second axis was 7.43, which can be considered as reasonably low values. The stream sites were first separated according to their location (latitude and temperature). The sites were further separated according to water level and nutrients, particularly N and P in surface and groundwater along axis 1 and water level along axis 2 (Appendix S4). Plant species composition for each stream individually is presented in Figure 5 and Appendix S5. The environmental variables that were most correlated with alterations in species composition differed across the five streams. In four of five streams, the x-axis appears to represent plant species composition in relation to position along the riparian gradient, while the y-axis depicts differences in composition between the control and flooding sections. The Verloren beek Oosterhuizen and Boye sites showed the clearest shift in species composition following the flooding treatment; at the flooding sections, plots at positions 2 and 1 shifted towards the "wetter" end of the first axis, thereby becoming more similar. Examples of species belonging to the "wetter" component are *Equisetum arvensis*, *Stachys palustris*, *Typha latifolia* and *Scirpus sylvaticus*. In contrast, the species composition at position 3 became more dissimilar compared to position 1.

3.6 | Similarity between seed and adult species composition along the stream riparian gradient

The species compositions of the existing riparian vegetation and the deposited seeds were strikingly different for the four investigated streams in 2011, after the first experimental flood (Voel bæk, Sandemandsbækken, Groote Molenbeek and Boye, Figure 6). In all cases,

TABLE 3 Summary of output from linear mixed models

Variables	Species richness (vegetation)	Biomass (aboveground vegetation)	Available N (soil)	Available P (soil)	Seed deposition (species richness)	Seed deposition (numbers)
Intercept	<0.001 (−)	<0.001 (−)	0.025 (+)	0.002 (+)	0.004 (−)	0.000 (−)
Temperature	0.098	<0.001 (+)	0.273	0.818	0.095	0.028 (+)
Extractable soil N	0.006 (−)	0.896	NA	0.001 (+)	NA	NA
Extractable soil P	0.165	0.001 (+)	0.000 (+)	NA	NA	NA
Groundwater N	0.116	0.426	0.861	0.298	NA	NA
Groundwater P	0.849	0.809	0.583	0.155	NA	NA
Biomass	<0.001 (−)	NA	0.073	0.002 (+)	0.73	0.825
Water level	0.001 (−)	0.147	0.061 (+)	0.019 (+)	0.001 (+)	0.118
Section	0.135	0.789	0.459	0.716	0.477	0.918
Section × Water level	0.062 (+)	0.033 (−)	0.223	0.828	0.482	0.806

NA, not applicable.
p-Values are given
Plus or minus symbols between brackets indicate whether a significant relation is positive or negative. Relationships represent overall relations (both flooding and control section results were included).
Statistical details are given in Appendix S3

the first axis of the CA separated the species composition in relation to the existing vegetation or the deposited seeds, while species composition relative to the position along the riparian gradient was separated along the second axis. Within the existing vegetation and the deposited seeds, a distinct gradient in species composition was detected corresponding to the hydrological gradient across the riparian zone. For all four streams, the majority of species were observed only in either the vegetation or the deposited seeds. The composition of newly established species in the flooding sections (determined in the year 2013) did match substantially to the composition of deposited seeds (found in the first experimental year 2011). An average of 26% of on average 18 newly established species corresponded to the deposited seeds. Examples of these species are *Mentha aquatica*, *Holcus lanatus*, *Rumex* as well as *Epilobium* spp.

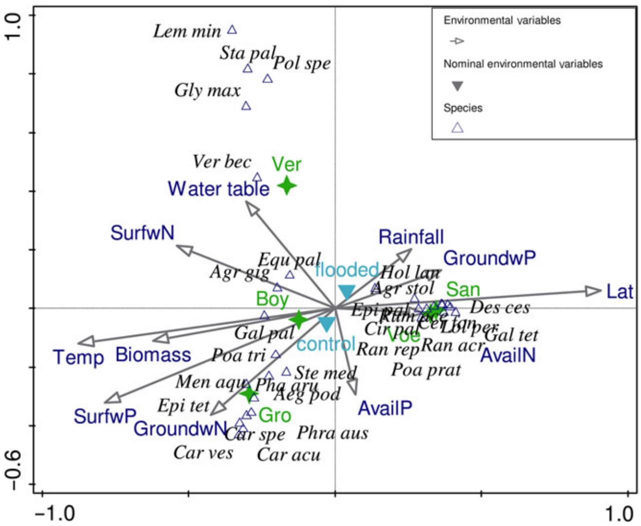

FIGURE 4 Distribution of plant species and sites along two canonical axes at the end of the flooding experiment (2013). Abbreviations of stream names: Voe = Voel bæk, San = Sandemandsbækken, Ver = Verloren beek Oosterhuizen, Boy = Boye, Gro = Groote Molenbeek. Variables: SurfwN = N in surface water, SurfwP = P in surface water, GroundwN = N in groundwater, GroundwP = P in groundwater, AvailN = extractable soil N, AvailP = extractable soil P, Lat = latitude, Temp = mean temperature. The 30 most abundant species are indicated with abbreviations; see Appendix S5 for a complete species list. [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our field experiment demonstrated that increased duration and depth of late winter/early spring flooding already affect the riparian vegetation in only 3 years of manipulation. Particularly at the lowest elevations along the riparian gradient, a shift in species composition was detected towards species more characteristic of regularly flooded, "wetter" conditions, such as for instance *Equisetum arvensis*, *Stachys palustris*, *Typha latifolia* and *Scirpus sylvaticus*. In addition, a decline in average species richness and an increase in average aboveground plant biomass were observed where the extent of flooding was increased. Within a time span of 3 years, a negative relation was observed between species richness and water levels in the experimentally flooded sections. A reciprocal transplantation study in Sweden in which effects of increased flooding were monitored over 6 years showed similar trends: A significant loss of riparian plant species and an increase in biomass occurred in turfs transplanted to lower elevations (Ström et al., 2011). Such rapid shifts in species composition are far more rapid than the decade timescales previously anticipated (Ström et al., 2011).

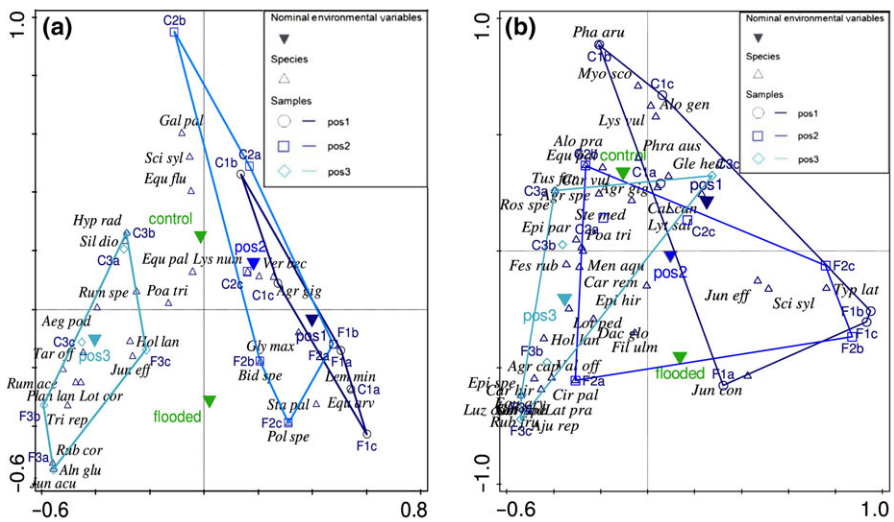

FIGURE 5 Plant species composition at the Verloren beek Oosterhuizen (a) and Boye (b) along two canonical axes. Correspondence analyses for the other streams are given in Appendix S6. The first two axes are correlated with position along the stream riparian gradient (pos. 1: lowest position along gradient, pos. 3: highest position) and control *versus* flooding section. Plot extremes are demarcated by envelopes (dark blue: pos. 1, mid-blue: pos. 2, light blue: pos. 3). Abbreviations of plot names indicate treatment (F: flooding, C: control), position (1, 2. 3) and transect (a, b, c). See Appendix S5 for a complete species list. [Colour figure can be viewed at wileyonlinelibrary.com]

The manifested changes in species richness may be caused by the increased levels of extractable soil N and P, which resulted from the winter flooding treatment. Increased levels of extractable N and P measured early in the growing season may indicate a rise in available N and P for plant uptake during the growing season and are likely to explain the increased biomass. We did, indeed, observe a positive relation between biomass and extractable soil P. The rise in biomass, in turn, may have contributed to the lower species richness, via increased competition for light or random species losses (Bobbink, Hornung, & Roelofs, 1998; Hautier, Niklaus, & Hector, 2009; Stevens, Dise, Mountford, & Gowing, 2004; Suding, Collins, & Gough, 2005). Particularly, the enrichment with P, via deposited sediment, is expected to increase riparian nutrient availability following flooding (Beumer et al., 2007; Walls, Wardop, & Brooks, 2005). Despite the finding that extractable soil P did not correlate with sedimentation in our study, we still found a strong relationship with increased flooding. This might be explained by the fact that the deposited sediment was waterborne and carried with the stream before sedimentation, and during the transport, easy desorpable phosphorus may already have been released. Hence, phosphorus attached to sediment particles can be adsorbed to stronger adsorbents such as Fe^{3+} (ferric iron; Kronvang et al., 2009). Phosphorus bound to iron oxides may still be plant available if the sediment faces reduced conditions; iron is then reduced to ferrous iron and thereby releases phosphate (often called phosphorus mobilization).

Increased plant mortality due to flooding stress in the existing vegetation also probably played a role in the observed declines in plant diversity. Several studies have demonstrated that both the seedling and adult stages of many riparian plant species are sensitive to flooding stress (Fraaije, ter Braak, Verduyn, Breeman, et al., 2015;

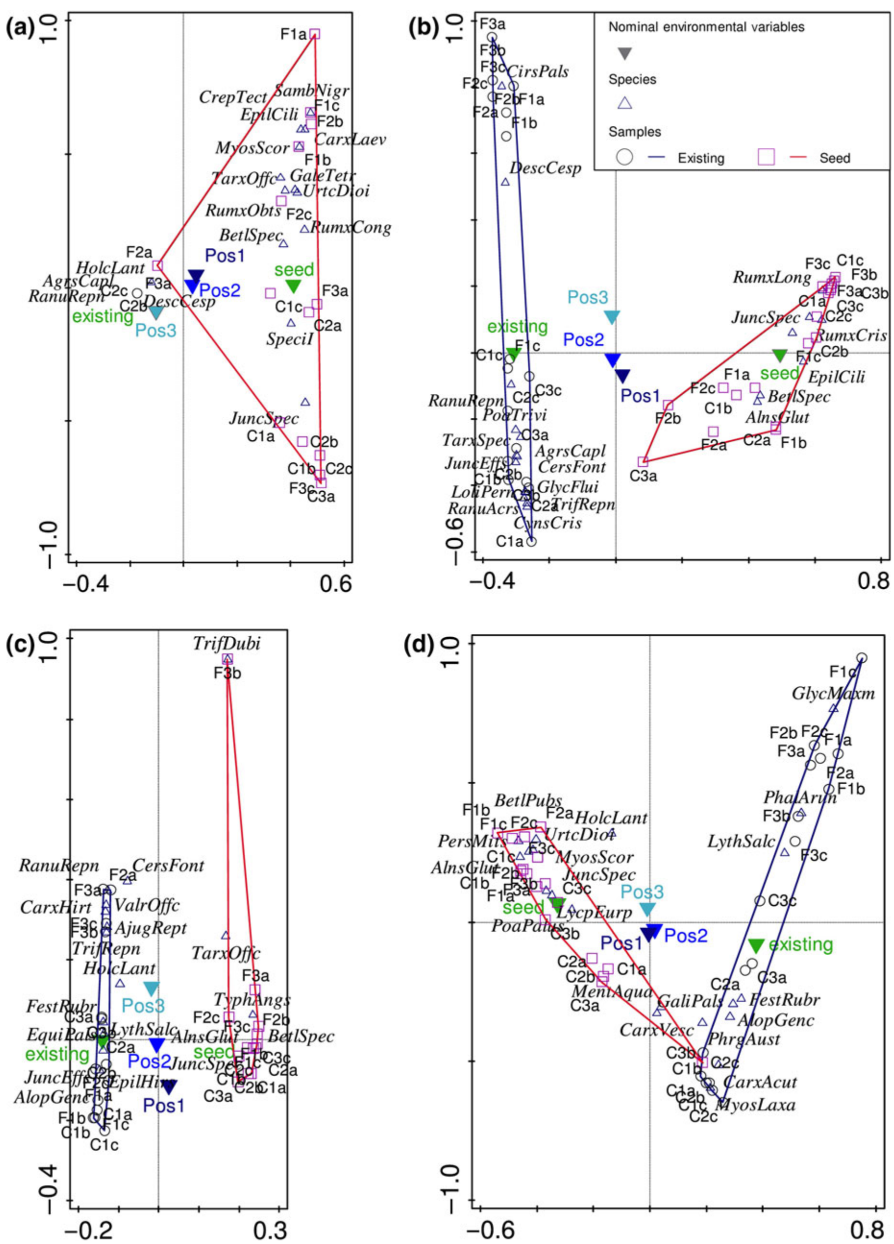

FIGURE 6 Species composition of adult plant communities and deposited seeds at the Voel bæk (a), Sandemandsbækken (b), Boye (c) and Groote Molenbeek (d) along two canonical axes. The first two axes are correlated with position along the stream riparian gradient (pos. 1: lowest position along gradient, pos. 3: highest position) and existing vegetation *versus* seeds. Plot extremes are demarcated by envelopes (dark blue: vegetation plots, red: seed traps). Abbreviations of plots indicate treatment (F: flooding, C: control), position (1, 2. 3) and transect (a, b, c). See Appendix S5 for a complete species list. [Colour figure can be viewed at wileyonlinelibrary.com]

Garssen et al., 2015; Sarneel & Soons, 2012; Voesenek, Van Oorschot, Smits, & Blom, 1993; Voesenek et al., 2004), and it is known that inundation is a driving factor for community assembly and species sorting along hydrological gradients (Fraaije, ter Braak, Verduyn, Verhoeven, et al., 2015; Silvertown, Araya, & Gowing, 2015; Silvertown et al., 1999). A diversity decline in the flooding sections is also not unexpected as there are more facultative than obligate wetland species. Our results demonstrated that overall, species turnover rates per plot were high and relative species turnover rates in the flooding sections were higher compared to the control sections. Across all five streams, on average four of the original six species per sampling plot disappeared between 2011 and 2013 in the flooding sections and were replaced by three new species (Appendix S2). Particularly, at the lowest elevation sampling points in the flooding sections, species losses on average exceeded species gain (2.7 species lost vs. 1.6 species gained), probably due to the strong flooding disturbance, while at the mid-elevation sampling points and all plots in the control sections, species losses and gains were more or less balanced.

Interestingly, the composition of the species pool of arriving seeds, from which new recruitments could originate, was very different from the species composition of the existing vegetation across the riparian zone in the first experimental year. We found evidence for the establishment of several deposited seed species in the riparian zone. On average, 26% of the newly established species composition in the flooding sections was equal to the species composition of deposited seeds found in the first experimental year. Most of the arriving seeds were deposited around the zero water level or average flood line, indicating that most seeds arrived via hydrochory (Soons et al., 2016). Thus, the majority of the arriving seeds appear to have been produced elsewhere, which may assist species turnover following local plant mortality. However, previous studies have indicated that the majority of species arriving in riparian seed traps are common species whose identity depends upon agricultural catchment use (Baattrup-Pedersen et al., 2013; Lorenz & Feld, 2013) and that the arrival of rare riparian wetland species is a limiting factor in their ability to colonize newly suitable sites (Baattrup-Pedersen, Riis, & Larsen, 2013; Brederveld, Jaehnig, Lorenz, Brunzel, & Soons, 2011). The latter two factors may explain why species recruitment following plant mortality was insufficient to maintain the original species richness levels, at least within the three-year timeframe of the experiment.

4.1 | Implications for management

Rapid and consistent changes in riparian plant species communities in response to increased duration and depth of winter flooding are likely to occur, resulting in an "upslope migration" of the zone of riparian species typical for very wet, regularly flooded conditions. Over a short time span of only a few years, this is expected to result in a reduction in riparian species richness, likely to be attributed in part to (1) species losses corresponding to the increased nutrient availability and plant biomass production (Hautier et al., 2009), and (2) species losses as local plant mortality leads to the replacement of rare or typical established plant species by common species. This implies that particularly in riparian zones in more heavily modified (agricultural) catchments, increased late winter/spring flooding may threaten communities that are sensitive to eutrophication (such as the habitats from the Habitats Directive listed in Appendix S1; Baattrup-Pedersen, Andersen, Larsen, Nygaard, & Ejrnæs, 2012). This negative response may be alleviated by measures at the catchment scale (Verhoeven, Soons, Janssen, & Omtzigt, 2008), including the preservation and/or restoration of wide and gradually sloping riparian zones, the improvement of stream and upland water quality (reduced nutrient loading) and the conservation of sufficient source populations of typical and rare riparian species.

ACKNOWLEDGEMENTS

The authors thank the water boards Peel en Maasvallei, Vallei en Veluwe, Emschergenossenschaft/Lippeverband, Staatsbosbeheer and Natuurmonumenten for permission to carry out experiments and help with the fieldwork. We thank G.A. Kowalchuk for valuable comments on the manuscript, and many colleagues and students for their assistance during experimental work. C.E. Juncu (Cathalina Communications) is recognized for her editorial advice. This research was funded by the EU 7th Framework Project REFRESH, contract no. 244121 and the company AstroTurf® (who sponsored seed mats).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Garssen AG, Baattrup-Pedersen A, Riis T, et al. Effects of increased flooding on riparian vegetation: Field experiments simulating climate change along five European lowland streams. *Glob Change Biol*. 2017;23: 3052–3063. https://doi.org/10.1111/gcb.13687