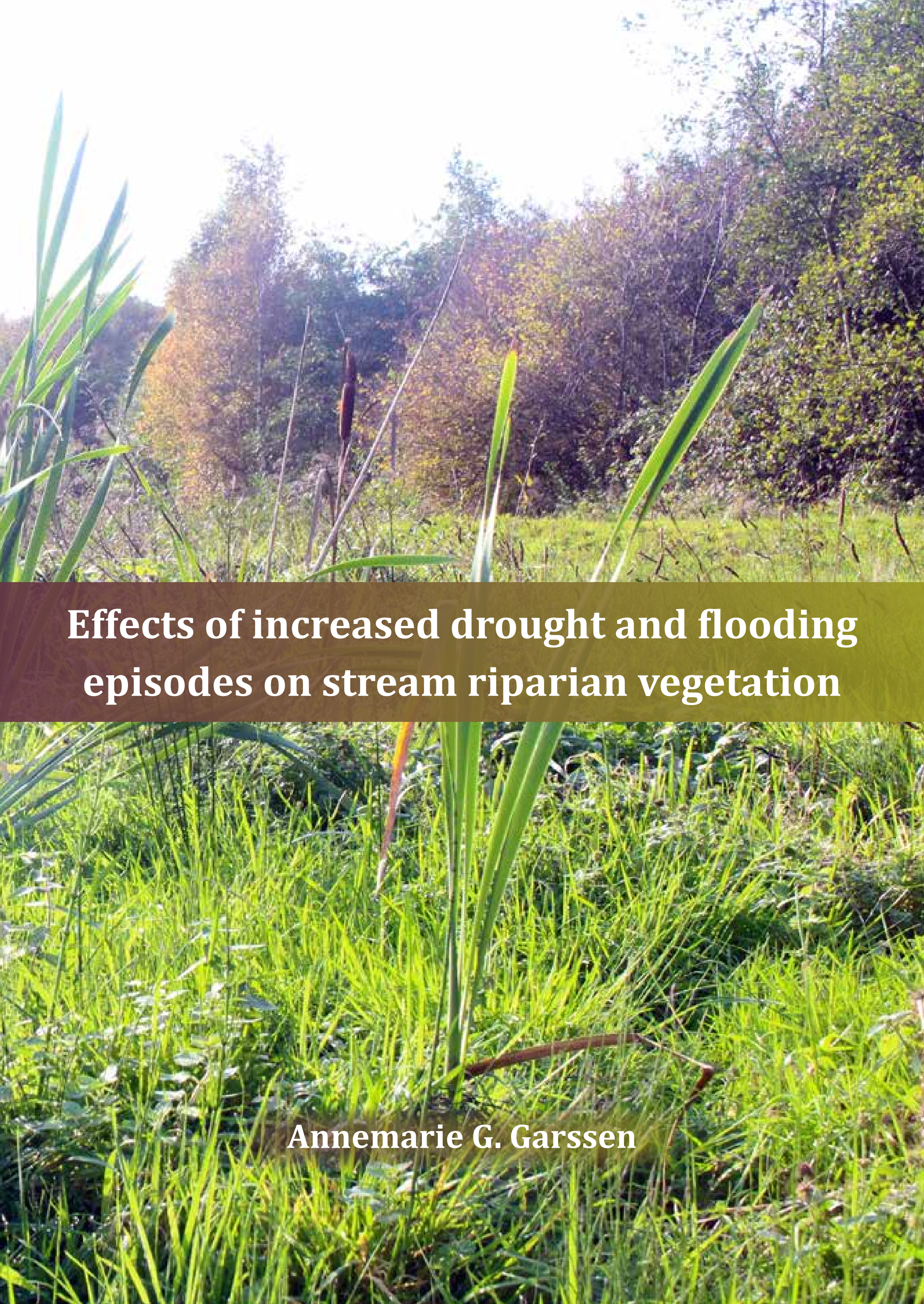


Effects of increased drought and flooding episodes on stream riparian vegetation

Annemarie G. Garssen

Effects of increased drought and flooding episodes on stream riparian vegetation

Annemarie G. Garssen

Thesis committee:	Dr. L. Bakker Prof. dr. ir. P. van Bodegom Prof. dr. H. Brix Prof. dr. ir. P.F.M. Verdonschot Prof. dr. L.A.C.J. Voesenek

Photo courtesy of: A.G. Garssen
Layout and printing: Print Service Ede, Ede, the Netherlands

ISBN: 978-90-83027-69-2

This thesis should be cited as:
Garssen A.G. (2019) Effects of increased drought and flooding episodes on stream riparian vegetation. PhD thesis. Utrecht University, Utrecht, the Netherlands.

Effects of increased drought and flooding episodes on stream riparian vegetation

De effecten van toenemende droogte en overstromingen op beekbegeleidende vegetatie

(met een samenvatting in het Nederlands)

Proefschrift

ter verkrijging van de graad van doctor aan de
Universiteit Utrecht
op gezag van de
rector magnificus, prof.dr. H.R.B.M. Kummeling,
ingevolge het besluit van het college voor promoties
in het openbaar te verdedigen op

maandag 9 december 2019 des ochtends te 10.30 uur

door

Annemarie Geertruida Garssen

geboren op 9 september 1982
te Vorden

Promotores: Prof. dr. M.B. Soons
Prof. dr. J.T.A. Verhoeven

This study was supported by the European Union 7th Framework Project REFRESH under contract no. 244121.

Contents

Chapter 1

General Introduction

Stream riparian wetlands

The temporarily flooded zones along streams, often defined as stream riparian wetlands (Naiman et al., 2003; Ström et al., 2011a), are of great ecological importance since they harbour a large number of characteristic plant and animal species (Sabo et al., 2005; Jansson et al., 2005). This high biodiversity is caused by strong environmental gradients in wetness, sediment quality and nutrient availability, resulting in mosaics of habitats providing niches for distinctive plant and animal species (Naiman et al., 2005; Naiman et al., 1993). Stream riparian wetlands are, by definition, tightly hydrologically connected to a stream, which itself forms a hydrologic system within a catchment. This system transports water, sediment and nutrients downstream, but also provides a bidirectional corridor for movement of riparian plant and animal species (Naiman & Décamps, 1997). In addition, riparian wetlands connect the surrounding uplands to the stream by transferring runoff and (shallow) groundwater, including nutrients. Due to their topographic position and hydrological connections, riparian wetlands provide many ecosystem services. They are particularly important for their buffering capacity during periods of heavy rainfall or drought, when they store or release water to the stream system, and for their ability to remove nutrients from the surface water (Richardson et al., 2007; Verhoeven et al., 2006; Capon et al., 2013). As mentioned above, they also provide a unique type of habitat for many plant and animal species and serve as corridors for plant and animal dispersal (Soons, 2006; Verhoeven et al., 2008).

Freshwater ecosystems including stream riparian wetlands are currently globally under threat, mainly due to their modification, fragmentation and pollution and to climate change (Naiman & Décamps, 1997; Hefting et al., 2006; Verhoeven et al., 2006). Worldwide, streams have been and are being modified for the purpose of flood control, agricultural activities and drinking-water abstraction (Mattingly et al., 1993; Malmqvist & Rundle, 2002). Between 1920 and 1970 more than 90% of all lowland streams in the Netherlands, Denmark and Britain have been channelized (Verdonschot & Nijboer, 2002), resulting in the loss of riparian wetlands and a strong reduction of hydrological functioning and species inhabiting the streams and adjacent zones, such as macroinvertebrates and riparian vegetation. Nowadays, stream restoration projects aim to restore riparian zones and ecosystem services (Fraaije, 2016).

Riparian plant communities are particularly influenced by gradients of water availability and fluvial disturbance (Merritt et al., 2010). Physical processes, such as stream flow regime and geomorphology strongly govern riparian vegetation composition, structure and abundance. Also, there is a strong linkage between a stream's natural flow regime and the trait composition of riparian vegetation (Lytle & Poff, 2004; Merritt et al., 2010). Riparian plant species may use different modes of adaptation to flow regimes in response to changes in frequency, magnitude and predictability of flooding, retraction and drought events, such as morphological, phenological and life history adaptations (Lytle & Poff, 2004; Merritt et al., 2010). Dispersal via water, hydrochory, is a dominant dispersal vector in riparian habitats. Several studies have shown that hydrochory plays a major role in dispersing and depositing seeds along river and stream corridors (Merritt & Wohl, 2002; Boedeltje et al., 2003; Gurnell et al., 2008; Soons et al., 2017). Hydrochory is considered important for the preservation of the high diversity characteristic for riparian plant communities by providing seeds from sites upstream (Nilsson et al., 1994) and through long-distance and directed dispersal (Merritt & Wohl, 2002; Soons et al., 2017; De Jager et al., 2019).

Stream riparian wetlands are expected to be sensitive to projected changes in climate, particularly to changes in temperature and precipitation. It is expected that changes in flow regimes driven by climate change, will have a considerable impact on riparian vegetation. However, there are large uncertainties regarding the extent to which climate change influences riparian plant species diversity and composition in the near future and the importance of different possible drivers of change. Research is crucial to unravel the effects of extreme events, such as drought and flooding episodes, on riparian plant species diversity and composition and formulate recommendations for future preservation and restoration of these ecosystems. The studies described in this thesis aim to make a contribution to such insights.

Climate change

The definition of climate change used by the International Panel on Climate Change (IPCC) is: “a change in the state of the climate that can be identified (e.g. using statistical tests) by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer. It refers to any change in climate over time, whether due to natural variability or as a result of human activity”. Nowadays, many researchers recognize climate change as the largest forthcoming threat to biodiversity in most biomes (IPBES, 2019; MEA, 2005), also affecting freshwater wetlands (IPBES, 2019; IPCC, 2007). It is widely recognized that climate change can have significant impacts on local and regional climatic regimes, affecting temperature, rainfall, river flows and water resources (Dankers & Feyen, 2009; Arnell & Reynard, 1995; IPCC, 2013).

There is compelling evidence that species are shifting their ranges in response to climate change (Walther et al., 2005; Lavergne et al., 2006), on small or larger scales. Next to changes in distribution, impacts of climate change on plant species include changes in population size, phenology and physiology (Hughes, 2000; Parmesan, 2006; Thuiller, 2005). Functional trait characteristics of plant species, such as seed buoyancy, but also vegetative traits such as root porosity or specific leaf area, will likely determine the species' ability to survive under altered environmental conditions (Jung et al., 2009). Some of these traits indicate a capability of early response to environmental change, including climate (Merritt et al., 2010).

Increased temperature and drought

Temperatures are expected to rise globally (IPCC, 2013). The IPCC summarizes this as follows: "The global mean surface temperature change for the period 2016–2035 relative to 1986–2005 will likely be in the range of 0.3°C to 0.7°C (medium confidence)". According to the IPCC, the increase of global annual mean surface temperatures for 2081–2100 relative to 1986–2005 is projected to likely be 0.3°C to 4.8°C. There are more frequent hot and fewer cold temperature extremes predicted over most land areas on daily and seasonal timescales as global mean temperatures increase. All these changes are not expected to be evenly distributed across the globe (Fig. 1.1), and for Europe intermediate levels of warming are projected (2.3°C to 2.7°C change, for 2081–2100 relative to 1986–2005, 50th percentile value),

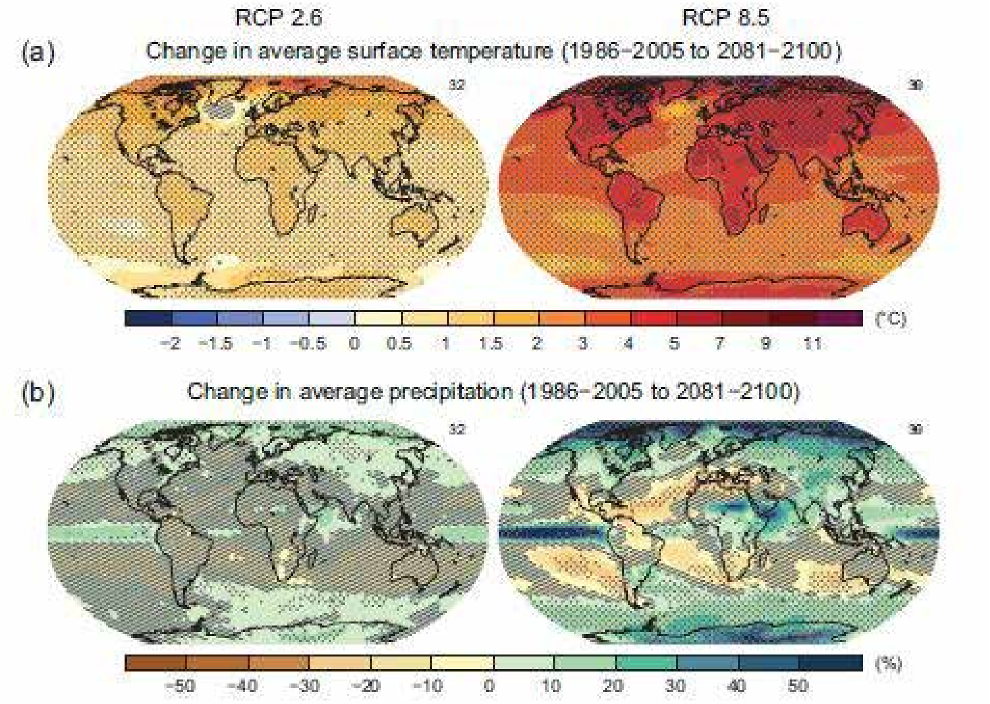


Fig. 1.1. Maps of CMIP5 multi-model mean results for the scenarios RCP2.6 and RCP8.5 in 2081–2100 relative to 1986-2005 of (a) annual mean surface temperature change, and (b) average percent change in annual mean precipitation. From IPCC, Fifth assessment report: Climate change 2013, The Physical Science Basis (Fig. SPM.8).

with clear distinctions among regions within Europe. Average annual precipitation is projected to decrease in Southern Europe, especially during summer (-11% change, for 2081–2100 relative to 1986–2005, 50th percentile value). The most pronounced changes for heatwave frequency and duration are expected to occur in southernmost Europe, while further north heatwave amplitude is expected to change profoundly (Fischer & Schär, 2010). An example of such an extreme episode was the European drought and heat wave in 2018; a period of unusually hot weather that led to record-breaking temperatures in many parts of Europe during the spring and summer of 2018. Higher summer temperatures will lead to more drought periods in and along streams. Also, summer precipitation is projected to occur more often in peaks, with longer periods in between these peaks, leading to increased drought.

Increased precipitation and flooding events

Rainfall patterns are expected to change globally (IPCC, 2013). In general, the contrast in precipitation between wet and dry regions and between wet and dry seasons is expected to increase, leading to increased drought and flooding episodes, although there may be regional exceptions. These precipitation changes are not expected to be evenly distributed across Europe and is projected to increase in Northern Europe, especially during winter (+11% change, for 2081–2100 relative to 1986–2005, 50th percentile value). As lowland streams and their adjacent zones are mainly rain-fed, these changes are expected to have significant effects on the hydrological interaction between streams and riparian zones, with implications for the ecology of both ecosystems.

Climate effects on nutrients

Climate change will not only affect riparian wetlands directly, but also indirectly by influencing biogeochemical cycles which control plant nutrient availability. Nitrogen and phosphorus cycling are especially important processes in the riparian zone, since nitrogen and phosphorus are the main nutrients controlling the growth of riparian plant communities. The capacity of riparian zones to retain nutrients such as nitrogen and phosphorus is controlled by hydrologic characteristics as well as biotic processes such as plant uptake and denitrification (Naiman et al., 2005). Biogeochemical processes (of phosphorus and nitrogen cycling), are limited by water or oxygen availability (Hefting, 2013). Changes in precipitation patterns caused by climate change influence inundation and discharge levels of streams and may stimulate the nutrient-rich input from agricultural pastures (run-off and leaching), thereby increasing nutrient input to stream-riparian zones.

During dry periods, mineralization occurs due to rising oxygen content, which in general leads to a higher availability of nitrogen. At the same time, iron (hydr) oxides may capture phosphates and decrease phosphate availability (Lucassen et al., 2005). When soils become flooded by surface water, increased sedimentation may add nutrients to the riparian zone. At the same time, the soil becomes almost completely anaerobic (Mitsch & Gosselink, 2015) and changes in pore water chemistry occur in the upper layer (Beumer et al., 2007). Anaerobic conditions increase reduction processes taking place in the soil, which are key factors for all nutrient flows. During anoxic conditions denitrification occurs, in case nitrate is available as an electron acceptor. Especially an anoxic environment rich in organic matter creates optimal conditions for denitrification, which leads to a considerable nitrogen removal potential (Hefting, 2003). As a consequence, in general the nitrogen availability will decrease during a period of flooding, but the speed of denitrification depends on available organic material, temperature, oxygen content and acidity. During periods of flooding, phosphate release from the top layer may increase in wetlands via the interference with sulphur and iron biogeochemistry in the subsoil. Sulphides which are formed by sulphate reduction, may loosen the iron-phosphorus bonds and cause phosphate release (Smolders et al., 2010). This so called internal eutrophication has led to a strong decline of the biodiversity in wetlands during the last decades.

REFRESH project

Climate change is expected to have a large impact on freshwater ecosystems, influencing hydrological, biogeochemical and biotic processes and, eventually, ecosystem biodiversity and services. Prediction of the mechanisms and consequences of this impact was the major focus of the research project REFRESH 'Adaptive Strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems', which was funded by the European Union's 7th Framework Programme. This large collaborative project with 25 partner institutes brought together rivers, lakes and wetlands scientists with expertise in hydrology, hydrochemistry and ecology, aquatic modelling and social science to study the effects of climate change in lakes, streams, rivers and wetlands across climatic gradients in Europe. The key objective of REFRESH was to develop a framework that enables water managers to design cost-effective restoration programmes for freshwater ecosystems (REFRESH, 2014a) to mitigate the expected future impacts of climate and land-use change.

My PhD research was conducted within the context of REFRESH, focussing on stream riparian wetlands, which are often influenced by human activities (mostly agriculture and urbanisation), and are thereby often highly modified and fragmented. I studied the two principal climate-related and interacting pressures: 1) increasing temperature, and 2) changes in water levels and flow regimes; while taking into account that European freshwater wetlands are often also confronted by excess nutrients. The aim was to provide new insights and strategies for water managers to apply cost-effective restoration programmes for freshwater ecosystems in the context of the European Union Water Framework Directive and the Habitat Directive. My research focused on riparian wetlands and aimed at identifying the main, short-term effects (including magnitude and direction of effect) of changes in temperature and precipitation on riparian wetland hydrology, plant species composition and functioning (REFRESH, 2014b). In the box below the objectives of REFRESH are shown that were related to my PhD study on stream riparian wetlands.

The following specific objectives of REFRESH were related to this PhD research;

- to understand the processes that govern the relationship between temperature, hydrology (and salinity) and nutrient/organic matter loading and the structure, function and biodiversity of freshwater ecosystems;
- to develop methods for identifying thresholds and reference conditions for systems facing climate change.

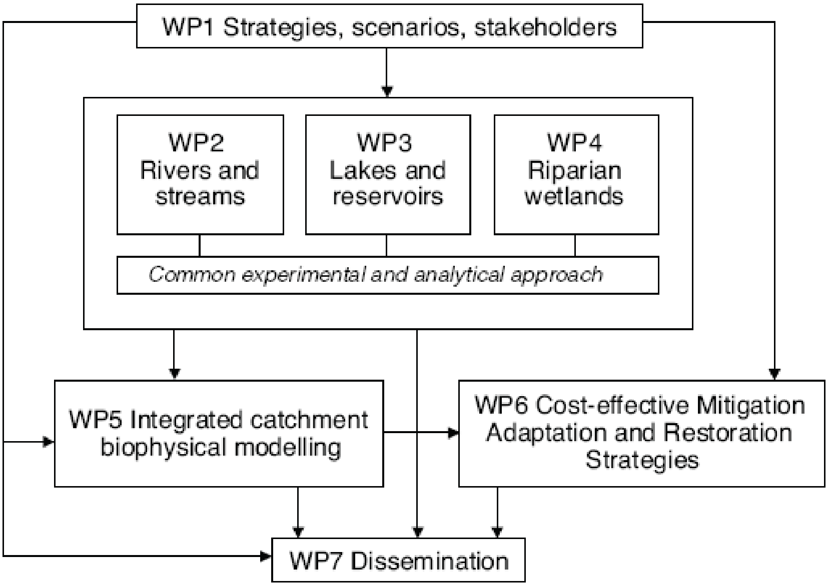


Fig. 1.2. Work package structure and connectivity within REFRESH project.

REFRESH consisted of in total seven work packages (Fig. 1.2). Partners working on Work Package 4 (WP4), studying riparian wetland functioning and biodiversity, included universities and institutions in the Netherlands, Denmark, Germany, and Spain. Within the context of the project we selected two main components of climate change which have been well-studied and are of direct relevance to stream riparian plant communities: temperature and precipitation. We investigated the effects of changes in temperature and precipitation in experimental studies, by manipulating stream and riparian zone hydrology across a climatic temperature gradient in Europe. In that way we aimed to simulate climate extremes; increased summer droughts and winter floods at different regional temperatures. In addition to the experimental work, my PhD study also comprised two meta-analyses on the effects of increased drought and flooding episodes on stream riparian vegetation, with a focus on riparian plant seedling survival, seed deposition, biomass, species composition and richness.

The effects of climate change on riparian wetlands along streams were investigated with an approach using the concept of the ‘Stream Riparian Gradient’, which ranges from the centre of the stream in its summer bed to the furthest point in the stream valley that can be flooded by surface water during winter floods (Verry et al., 2004). We chose this approach since this gradient includes the locations that are most influenced by changes in surface water and groundwater levels during drought and flooding events. For practical purposes, we more narrowly defined stream riparian wetlands as that part of the Stream Riparian Gradient that ranges from the lowest water level of the stream under summer base flow to the furthest point up the stream valley that can be flooded by surface water during extreme winter floods (the floodplain or flood-prone area). This excludes the part of the stream permanently carrying water (the summer bed) (Fig. 1.4c.).

Methods field experiments

Full-scale field simulation experiments along streams were carried out in the Atlantic European climate zone, in Denmark, Germany, The Netherlands and Spain (Fig. 1.3). To standardize the experimental set-up across sites, the experimental riparian wetlands were selected according to a set of criteria, to represent small lowland streams in agricultural landscapes. They are characterized as follows:

1) lowland stream, with a gentle slope (< 1 m/km);
2) V-shaped stream valley with a gradually sloping riparian zone;
3) sandy substrate;
4) stream hydrology driven by precipitation, but discharge pattern relatively stable over the year, with (summer) flow permanence and not characterised by extreme (winter/spring) spates, no lake outlets;
5) stream order 2-3, with width approximately 3-5 m;
6) open (non-forested) wetland vegetation in the riparian zone without history of recent fertilization, restoration, or management of ditch cleaning.

We selected streams according to the criteria above along a temperature gradient across Atlantic Europe, from Denmark (DK), via West Germany (D), the Netherlands (NL) to Atlantic Spain (A-ES) (Fig. 1.3 and Table 1.1).

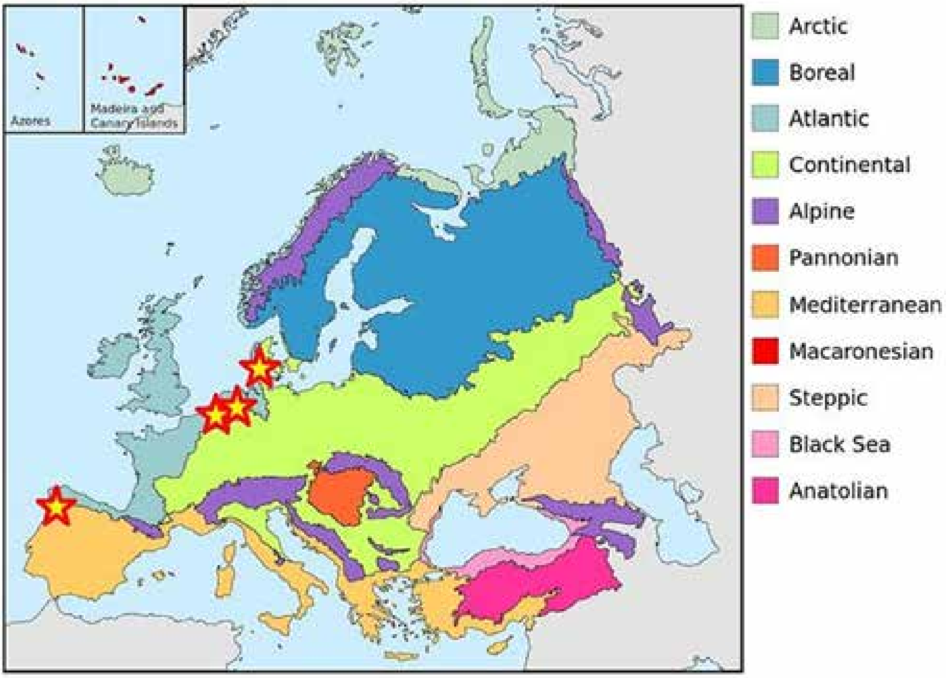


Fig. 1.3. Locations of the experimental stream riparian wetland sites along a temperature gradient across Atlantic Europe. Biogeographical regions are indicated in the legend. Map from the European Environment Agency (www.eea.europa.eu).

Sites were selected to have similar precipitation characteristics, so that experimental manipulations of stream water tables representing expected changes in precipitation patterns would be comparable between sites (temperature varies between sites, hydrology varies between treatments within each site, Table 1.1). In the stream riparian wetlands, summer drought or winter flooding were simulated by creating water diversions out of, or towards the experimental section of the wetland, respectively, using dams and/or bypasses. In summer, prolonged drought periods were simulated for 10 weeks from July to mid-September. In winter, prolonged flooding periods were simulated for 6 weeks in February and March, resulting in an increase in water levels. All treatments were applied for three consecutive years, except in Spain where treatments were applied for only one year. Experimentally treated sections were compared to similar, unmanipulated control sections to quantify effects (Fig. 1.4). Data collection for this PhD study was carried out for stream and riparian wetland hydrology (water levels), water quality (nutrients), riparian vegetation biomass, species composition and diversity, seed rain and nutrient cycling (nitrogen and phosphorus availability).

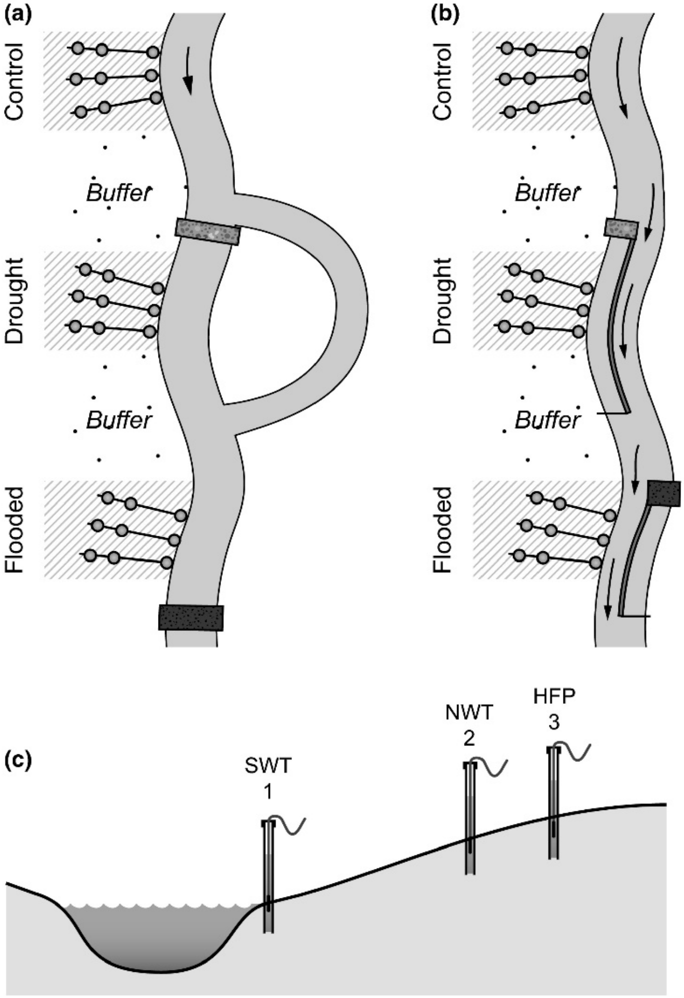


Fig. 1.4. A schematic presentation of the experimental setup applied in our study (from Baattrup et al., 2018). Flooding was created by constructing dams (marked as bars on the figure) to obstruct the water flow in the main channels. (a) In Denmark, a lateral dam of sandbags was constructed across the stream channel. (b) In Germany and the Netherlands, longitudinal dams were built within the channel, which together with a lateral dam across the channel obstructed the water flow in the main channel. (c) The position of the sample transects within the experimental sections. The first piezometer was placed just above the summer water table (position 1), the second piezometer just above the normal winter water table (position 2) and the third at the high end of the floodplain (position 3). The circles in panels a and b indicate the position of the piezometers along each transect.

Table 1.1. Names, locations and climate characteristics of the stream riparian wetland sites used for the experimental manipulations of drought and flooding.

Name	Country	Coordinates in lat/long	Average winter (Dec-Jan-Feb) – summer (Jun-Jul-Aug) temperature in˚C	Average winter (Dec-Jan-Feb) – summer (Jun-Jul-Aug) precipitation in mm/ month	Drought experiments	Flooding experiments
Voel baek	DK	56°19›58.46” N 9°70›39.32” E	0.88-15.56	20.67-28.39	3 years	3 years
Sandemands-baekken	DK	56°15’85.07”N 9°49’61.20” E	2.01-15.49	21.64-28.86	3 years	3 years
Boye	D	51°58’61.13”N 6°91’10.01”E	2.58-18.05	62.68-90.16		3 years
Verloren beek Oosterhuizen	NL	52°15’91.13”N 6°02’11.54”E	2.55-16.94	71.38-98.90		3 years
Groote Molenbeek	NL	51°39’17.32”N 6°03’59.47”E	2.73-17.74	61.15-82.90	3 years	2 years
Pego	A-ES	41°58’34.10”N 8°45’15.41”W	8.98-14.98	172.4-44.73	1 year	
Caselas	A-ES	42° 4’19.13”N 8°32’52.43”W	8.47-19.41	200.1-43.75	1 year	

Research objective

My research project aimed at identifying the main effects of climate-driven increases in summer drought and winter flooding episodes on the diversity and species composition of stream riparian plant communities. As detailed above, both hydrologic extremes (drought and flooding episodes) are expected to occur more often in the near future, albeit in different geographic regions. In this thesis, I aimed to disentangle the main effects of increased drought and flooding events on riparian plant communities. By studying the hydrological changes and biotic processes of vegetation along stream riparian zones along a climatic temperature gradient, I aimed for a better insight in the effects on riparian plant diversity and for providing recommendations for future conservation of these potentially highly diverse ecosystems. In particular, this research addressed the questions:

i) Will increased drought or flooding episodes lead to significant changes in species diversity and composition of stream riparian plant communities and what are important underlying mechanisms?
ii) How fast will these changes occur?
iii) What are the consequences for conservation and restoration?

Crucial factors were identified that have a positive or negative relation with plant species diversity. Specifically, I focused on the effects of increased drought and flooding on seed deposition and seedling survival, plant biomass and plant available phosphorus and nitrogen, since these factors may directly influence riparian plant species composition and diversity.

Thesis outline

The research approach included a combination of meta-analysis studies and field experiments focusing on the effects of increased drought and flooding episodes on stream riparian vegetation. Two meta-analysis studies based on quantitative literature data were conducted, the first with the aim to investigate effects of drought on riparian vegetation and the second with a focus on flooding effects. During three years a large field experiment in European stream riparian wetlands was conducted to investigate the effects of increasing and decreasing stream water levels on riparian plant biomass, phosphorus and nitrogen availability, seed deposition, species composition and diversity. Effects of drought and flooding episodes on plant taxonomic diversity and functional trait composition were explored.

Chapter 2 describes the outcome of a literature study and meta-analysis on the effects of an increase in summer drought on riparian plant species. It was our aim to consolidate existing quantitative information on effects of summer drought on riparian vegetation across the world, which was the main reason to choose a meta-analysis approach. The effects of increased drought on riparian seedling survival, plant biomass, riparian plant species composition and richness were studied. Factors determining species responses, such as specific plant traits, groundwater levels, and surface water permanence were considered in order to identify general trait-driven predictors of species responses to these global change drivers.

Chapter 3 focuses on the outcome of our experimental field experiments studying the effects of increased summer drought. This comparative field study focused on diversity and functioning of riparian vegetation along a European climatic gradient from Denmark to Atlantic Spain. During three consecutive years we observed the effects of lower water tables on plant biomass, species composition and diversity, as well as phosphorus and nitrogen availability and explored if there are similarities between sites in response to episodes of summer drought.

Chapter 4 describes a meta-analysis on riparian plant community responses to increased flooding. Riparian adult and seedling survival, plant biomass and plant species composition and richness responses to flooding were examined quantitatively. In addition, plant traits were reported that are of key importance for the response of riparian plant species to flooding and the effects of nutrient, climatic and hydrological status of the catchment were considered.

Chapter 5 reports on the experimental outcome of field experiments simulating increased flooding along five European lowland streams in Denmark, Germany and the Netherlands. We chose for this field setup since only very few studies have investigated flooding effects at the ecosystem level experimentally. The responses in riparian plant species richness, biomass, plant-available nitrogen, phosphorus and seed deposition to increased flooding depth and prolonged flooding duration were assessed.

Chapter 6 considers structural and functional responses of plant communities to climate change-mediated alterations in the hydrology of riparian areas in temperate Europe. Effects of drought as well as flooding episodes on plant taxonomic diversity and functional trait composition were explored in a large-scale field experimental approach in riparian areas in temperate Atlantic Europe. Trait-based predictions of the response of riparian communities are valuable since functional trait characteristics of plant species will likely determine whether species are able to survive during and after flooding or drought episodes.

In Chapter 7 a synthesis is presented of Chapters 2-6, and the results are placed in the context of current insights in riparian plant species responses to increased drought and flooding episodes in times of climate change. To conclude, the results are interpreted to recommendations for riparian wetland conservation and restoration in the near future.

Chapter 2

Effects of climate-induced increases in summer drought on riparian plant species: a meta-analysis

Annemarie G. Garssen, Jos T.A. Verhoeven and Merel B. Soons

Freshwater Biology (2014), 59, 1052–1063
doi: 10.1111/fwb.12328

Abstract

Frequency and duration of summer droughts are predicted to increase in the near future in many parts of the world, with considerable anticipated effects on riparian plant community composition and species richness. Riparian plant communities along lowland streams are characterized by high species richness due to their system-specific environmental gradients. As these streams and their hydrological gradients are mainly rain-fed, they are sensitive to precipitation changes.

We conducted a literature survey and meta-analysis to examine the effects of an increase in summer drought on: (i) riparian plant biomass; (ii) riparian seedling survival and (iii) riparian plant species composition and richness. We also aimed to determine whether hydrological thresholds related to drought tolerance can be distinguished for riparian plant species.

ISI Web of Knowledge was searched for relevant peer-reviewed studies, and 23 papers were found that met our criteria and contained quantitative study results. To detect overall responses of biomass and seedling survival, a random-effects model was applied using Comprehensive Meta-analysis™ software. Regression curves were then fitted to response ratio data relating the effects on drought impacted groups to those on control groups.

Our results showed that a drought duration of approximately >30 days strongly reduces riparian plant biomass and that a duration of approximately >30–35 days and high drought intensities (starting from 3 to 4 cm water table decline per day) can be detrimental for riparian seedling survival. Especially *Populus* and *Salix* seedlings showed a reduced survival in response to drought, in contrast to *Tamarix* seedlings, which have the ability to rapidly and expansively elongate their roots. The data also revealed that an increase in drought conditions rapidly leads to a decline of riparian species richness and an increased presence of species adjusted to drier conditions.

Riparian groundwater level, surface water permanence and certain plant traits, especially plasticity in rooting depth, were mentioned most frequently as factors determining species responses. Very few studies mentioned hydrological thresholds, such as critical values for ground- and/or surface water levels, and so far these results have proved difficult to generalize.

Our meta-analysis has shown that the projected increase in the duration and intensity of drought periods, especially intense droughts lasting more than 30 days, can be expected to narrow the riparian wetland zone with typical hydric species and accelerate riparian wetland species losses in the near future. This may require extra efforts in terms of management and restoration of species-rich riparian areas.

Introduction

Climate change is a considerable potential threat to biodiversity in most biomes, especially in vulnerable habitats (MEA, 2005). A warmer and at the same time more variable climate is expected to enhance the probability of extreme events such as droughts and floods (Wetherald & Manabe, 2002). Summer droughts are likely to become more intense in many parts of the world, due to a decrease in precipitation combined with an increase in evaporation in spring and summer (Wetherald & Manabe, 1999; Douville et al., 2002; Wang, 2005). Since the 1970s global aridity has increased substantially in most of Africa, southern Europe, East and South Asia and eastern Australia (Dai, 2011). A likely increase in persistent droughts is projected in the 21st century for most of Africa, southern Europe and the Middle East, most of the Americas, Australia and Southeast Asia (Dai, 2011). Climate change is expected to have a significant impact on lowland streams and their adjacent riparian zones, through local and regional changes in temperature and rainfall, which result in modified river and stream flows and wetland water regimes (Arnell & Reynard, 1996; IPCC, 2007; Dankers & Feyen, 2009).

Lowland streams are usually rain-fed systems and their riparian zones are often regarded as vulnerable due to their sensitivity to changes in precipitation and temperature (Decamps, 1993) and their overall impacted and degraded status around the world (Tockner & Stanford, 2002). However, Catford et al. (2013) suggested that riparian systems are resilient to climate change since they have evolved under conditions of hydrological extremes. Riparian wetlands, the temporarily flooded areas along rivers and streams, are of great ecological importance because they harbour a large number of distinctive plant and animal species (Naiman et al., 1993; Naiman & Decamps, 1997; Jansson et al., 2005; Sabo et al., 2005). Their high diversity is caused by multiple environmental gradients, resulting in mosaics of different habitats (Naiman et al., 1993). Moreover, riparian wetlands provide several important ecosystem services by storing and purifying water, preventing erosion, providing spawning habitat and nurseries for fish species and serve as corridors for plant dispersal (Naiman et al., 1993; Goodson et al., 2004; Sabo et al., 2005; Soons, 2006; Verhoeven et al., 2006, 2008; Richardson et al., 2007; Capon et al., 2013).

The projected decrease in summer precipitation and increase in evaporation can quickly lead to a reduction in soil moisture in summer (Manabe & Wetherald, 1987; Gregory et al., 1997; Wetherald & Manabe, 1999). Lower soil moisture can have adverse effects on plant life and may also decrease the supply of ground water by restricting capillary processes (Gregory et al.,1997). Several abiotic factors control soil moisture content, which is a very important habitat prerequisite for plants. Sediment type and particle size are important factors for the water-holding capacity of soils and determine the thickness of the capillary fringe, which can compensate for a deeper water table (Gonzalez et al., 2010). The lower the water-holding capacity of soils, the greater the sensitivity of plants to drought.

Documented responses of riparian plant species to drought conditions vary. These responses are influenced by both the duration and intensity of the drought period, as well as by specific plant species traits. Individuals may use plastic response mechanisms to cope with drought conditions, while species may undergo a range shift or adapt to the drought conditions in the long term. Individual plants can use several response mechanisms to cope with drought conditions. Most individuals will minimise the risk of desiccation by maintaining a favourable internal water content (Kozlowski & Pallardy, 2002) and use specific mechanisms to either increase water uptake or decrease water loss (Pallardy, 2008). Internal mechanisms, such as osmoregulation, can keep relative water content of the plant high to use water efficiently (Kozlowski & Pallardy, 2002). At times of water stress, plants can decrease their above-ground surface area and eventually biomass, thereby reducing water loss, or increase their rooting depth, thereby increasing water uptake. The seedling stage is considered vital in the rejuvenation and/or colonisation phase of a plant species, but is especially sensitive as seedlings are known to respond rapidly to changing abiotic conditions (Rood et al., 2008; Stella & Battles, 2010). Life-history strategies of plants (annual versus perennial life cycle for example) and mechanisms such as vegetative quiescence and seed dormancy also play a role in the resilience with respect to drought. In cases of severe drought when plant mechanisms are not sufficiently effective to tolerate drought, species are expected to be replaced by other, more drought-tolerant species, but the rate at which this occurs will be limited also by species' dispersal capacities (Brederveld et al., 2011).

So far, few studies have considered quantitative effects of summer drought on riparian vegetation. However, such information is needed to forecast changes in species composition and diversity of these potentially highly vulnerable ecosystems in the future. To quantify how riparian vegetation responds to summer drought, we addressed the following questions:

1. What is the relationship between duration of drought and riparian plant biomass? At what duration do negative effects on biomass start to occur?
2. What are the effects of duration and intensity of drought on riparian seedling survival? Can differences between riparian tree seedling species in drought tolerance be related to relevant plant traits?
3. What are the effects of an increase in duration and intensity of summer drought on riparian plant species composition and richness?
4. Can specific hydrological thresholds related to drought be distinguished for riparian plants?

In this study, we used a meta-analysis to assess the quantitative effects of drought on biomass, seedling survival and plant traits related to drought resilience. A literature survey was carried out to evaluate the effects of summer drought on species composition and diversity in riparian habitats along streams, to determine which species are sensitive and whether there are thresholds to be distinguished for the species. We focused on riparian zones along lowland streams outside of the tropics and subtropics.

Methods

We searched ISI Web of Knowledge for scientific peer reviewed studies on effects of (increased) drought on riparian wetland plant species. To efficiently extract relevant articles, we selected specific keyword strings for our search (see Table S2.1). Titles and abstracts were all checked for relevance using the following strict study eligibility criteria. We only selected data from field studies carried out in riparian wetlands along streams or rivers, or relevant mesocosm/greenhouse experiments, carried out with riparian wetland plants. Studies from tidal systems, estuaries or lakes were excluded. All selected studies had a before–after (BA), control–impact (CI) or a before–after–control–impact (BACI) design, to be able to quantify the effects of drought. We did not use results from studies on sites with a history of strong disturbance, such as the application of local fertilisation, ditch cleaning, or recent restoration. Studies conducted in the temperate Atlantic, Continental, Boreal and (Semi)-arid biogeographic regions (worldwide) were included. In practice, most of the studies included are of Northern Hemisphere systems, and we acknowledge that our analysis may be less directly applicable to Southern Hemisphere riparian zones with different riparian species, climate, soils, etc. A literature survey was conducted of papers reporting on the response of riparian plant species composition and richness to an increase in summer drought. Since too few quantitative results were provided in the papers regarding the effects of summer drought on species richness, we have undertaken a more classic review of the literature instead of conducting a meta-analysis for this topic. We extracted relevant details on the main trends and observations, responsible mechanisms, biogeographical region, research set-up and thresholds or indicator species. We summarised these details in a descriptive table (see Table S2.2). In the text below, we focus on the methods used in the meta-analysis that we used for responses of riparian plant biomass and seedling survival.

Plot Digitizer 2.6.1 software (Free Software Foundation, Inc., Boston, MA, U.S.A.) was used to extract data from graphs, in case data were not presented in tables. All available quantitative data were summarised in coding sheets for the species and community responses, as well as for the response variables plant total biomass and seedling survival. Extra information was included concerning the study system, plant communities, relevant plant traits and thresholds (e.g. biogeographical region, vegetation type and groundwater level). With a quantitative research synthesis, we analysed data from all selected study cases. The responses of plant total biomass and seedling survival to drought were calculated as the ratio of the treatment (or after situation; impact) and the control group (or before situation), since this ratio provides a relative quantification of the effect size, which is suitable for comparisons (Borenstein et al., 2005). A response ratio equal to 1 means no change, while a response ratio >1 indicates a positive change (increased biomass or survival), and a value <1 equals a negative change (decreased biomass or survival). To test whether there were any overall, significant effects of drought on biomass or seedling survival, we first used the software program Comprehensive Meta-analysis (CMA version 2.0, Biostat, Inc., Englewood, NJ, U.S.A.; Borenstein et al., 2005), which enabled us to assign weights required for random-effects analysis. For each response variable, the program calculated a two-group comparison for each study case by calculating the effect size. A random-effects model was applied since the true effect size varied from study to study. Study results were calculated in Effect Size metrics with 95% confidence intervals. Standardised mean differences were used, since all effect sizes needed to be transformed into a common metric to calculate an overall effect. A two-tailed Z-test was conducted to examine the null hypothesis (effect size equals zero).

To analyse more specifically the relation between duration and intensity of drought and the response ratio of biomass and seedling survival, we used the statistical package SPSS (IBM SPSS Statistics version 20, IBM, Amsterdam, the Netherlands) to fit linear or logistic weighted regression curves to the response data. We also looked at the relation between duration of drought and response ratio of seedling survival of three plant genera characteristic for riparian zones in the Northern Hemisphere: *Salix*, *Populus* and *Tamarix*. We calculated the R-squared and P-values of all weighted regression curves, to test whether relationships were significant.

Results

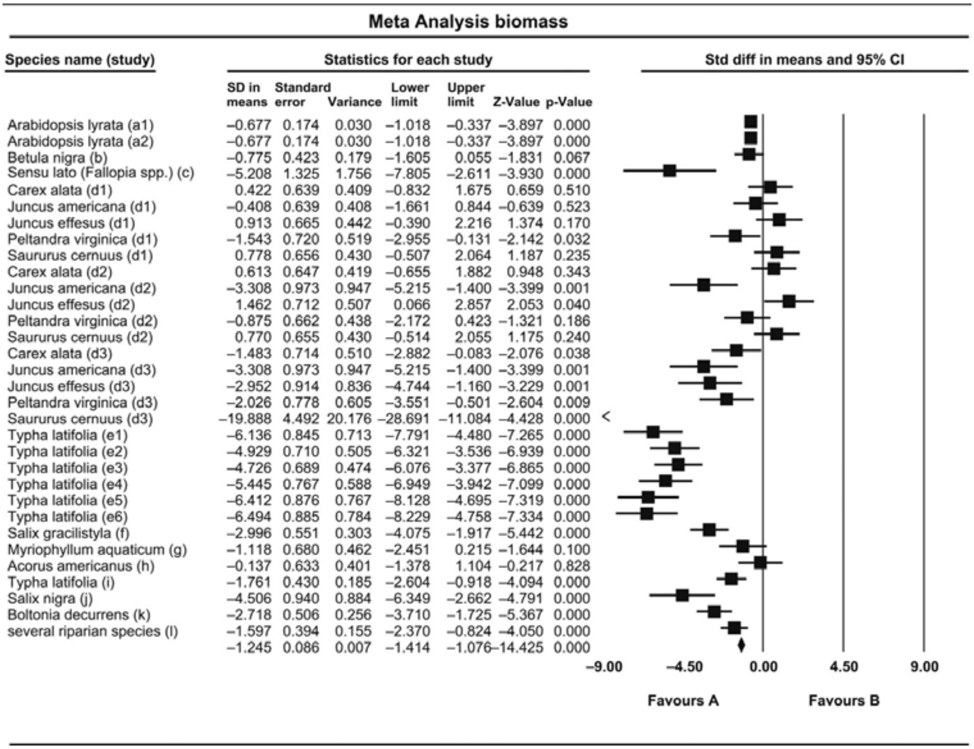
Our search query in Web of Science yielded 683 articles, of which only 23 met our thorough eligibility criteria and contained quantitative study results: 12 studies reporting on 32 cases regarding biomass, five studies reporting on 261 cases concerning seedling survival and four studies reporting on species richness.

Plant total biomass

The studies used for our analysis on plant total biomass ranged in drought conditions from very mild drought stress (plants received 400 mL water per day compared with a control of 800 mL water per day, e.g.) to severe drought stress (the plants were not watered at all and the wilting point was reached). The duration of the drought periods varied from 14 to 180 days. Despite this wide range of treatments, our meta-analysis confirms that there is a highly significant overall effect of drought on the amount of total biomass (dry weight) of riparian wetland plants (random-effects model, $P < 0.001$;

Table 2.1), which becomes critical when droughts last longer than approximately 30 days (Fig. 2.1). Since different species display a different tolerance to drought, a species list is included in Table 2.1. For shorter periods of drought, some response ratios had values >1, which indicates that there was an initial positive effect of drought on the performance (total biomass) of these species. These cases had a relatively wet control situation (water level 5 cm above substratum), so these particular species showed a more optimal response to dryer conditions. Furthermore, Fig. 2.1 shows that under more severe drought conditions, there is a relatively fast decrease in biomass, while there is a more gradual decrease in biomass when drought conditions are milder.

Table 2.1. Outcome of random-effects model meta-analysis on effects of drought on biomass (dry weight) of riparian plants. Standard differences (SD) in means with a negative value ('Favours A') indicate a negative effect of drought on biomass in the respective study, while positive values ('Favours B') indicate a positive effect. Results of 32 cases are shown from the following sources (studies identified by letters in parentheses). Type of study: greenhouse experiments, except Hudon (2004) who performed a field experiment. Asamoah & Bork, 2010 (e); Hudon, 2004 (l); Hussner et al., 2008 (g); Kleczewski et al., 2012 (b); Li, Pezeshki & Goodwin, 2004 (i); Nakai et al., 2009 (f); Pezeshki et al., 1998 (j); Romanello et al., 2008 (h); Sletvold & Agren, 2012 (a); Smith et al., 1993 (k); Touchette et al., 2010 (d); Walls, 2010 (c). See reference section for complete references.



Meta Analysis biomass

Species name (study)	Statistics for each study						
	SD in means	Standard error	Variance	Lower limit	Upper limit	Z-Value	p-Value
Arabidopsis lyrata (a1)	−0.677	0.174	0.030	−1.018	−0.337	−3.897	0.000
Arabidopsis lyrata (a2)	−0.677	0.174	0.030	−1.018	−0.337	−3.897	0.000
Betula nigra (b)	−0.775	0.423	0.179	−1.605	0.055	−1.831	0.067
Sensu lato (Fallopia spp.) (c)	−5.208	1.325	1.756	−7.805	−2.611	−3.930	0.000
Carex alata (d1)	0.422	0.639	0.409	−0.832	1.675	0.659	0.510
Juncus americana (d1)	−0.408	0.639	0.408	−1.661	0.844	−0.639	0.523
Juncus effesus (d1)	0.913	0.665	0.442	−0.390	2.216	1.374	0.170
Peltandra virginica (d1)	−1.543	0.720	0.519	−2.955	−0.131	−2.142	0.032
Saururus cernuus (d1)	0.778	0.656	0.430	−0.507	2.064	1.187	0.235
Carex alata (d2)	0.613	0.647	0.419	−0.655	1.882	0.948	0.343
Juncus americana (d2)	−3.308	0.973	0.947	−5.215	−1.400	−3.399	0.001
Juncus effesus (d2)	1.462	0.712	0.507	0.066	2.857	2.053	0.040
Peltandra virginica (d2)	−0.875	0.662	0.438	−2.172	0.423	−1.321	0.186
Saururus cernuus (d2)	0.770	0.655	0.430	−0.514	2.055	1.175	0.240
Carex alata (d3)	−1.483	0.714	0.510	−2.882	−0.083	−2.076	0.038
Juncus americana (d3)	−3.308	0.973	0.947	−5.215	−1.400	−3.399	0.001
Juncus effesus (d3)	−2.952	0.914	0.836	−4.744	−1.160	−3.229	0.001
Peltandra virginica (d3)	−2.026	0.778	0.605	−3.551	−0.501	−2.604	0.009
Saururus cernuus (d3)	−19.888	4.492	20.176	−28.691	−11.084	−4.428	0.000
Typha latifolia (e1)	−6.136	0.845	0.713	−7.791	−4.480	−7.265	0.000
Typha latifolia (e2)	−4.929	0.710	0.505	−6.321	−3.536	−6.939	0.000
Typha latifolia (e3)	−4.726	0.689	0.474	−6.076	−3.377	−6.865	0.000
Typha latifolia (e4)	−5.445	0.767	0.588	−6.949	−3.942	−7.099	0.000
Typha latifolia (e5)	−6.412	0.876	0.767	−8.128	−4.695	−7.319	0.000
Typha latifolia (e6)	−6.494	0.885	0.784	−8.229	−4.758	−7.334	0.000
Salix gracilistyla (f)	−2.996	0.551	0.303	−4.075	−1.917	−5.442	0.000
Myriophyllum aquaticum (g)	−1.118	0.680	0.462	−2.451	0.215	−1.644	0.100
Acorus americanus (h)	−0.137	0.633	0.401	−1.378	1.104	−0.217	0.828
Typha latifolia (i)	−1.761	0.430	0.185	−2.604	−0.918	−4.094	0.000
Salix nigra (j)	−4.506	0.940	0.884	−6.349	−2.662	−4.791	0.000
Boltonia decurrens (k)	−2.718	0.506	0.256	−3.710	−1.725	−5.367	0.000
several riparian species (l)	−1.597	0.394	0.155	−2.370	−0.824	−4.050	0.000
	−1.245	0.086	0.007	−1.414	−1.076	−14.425	0.000

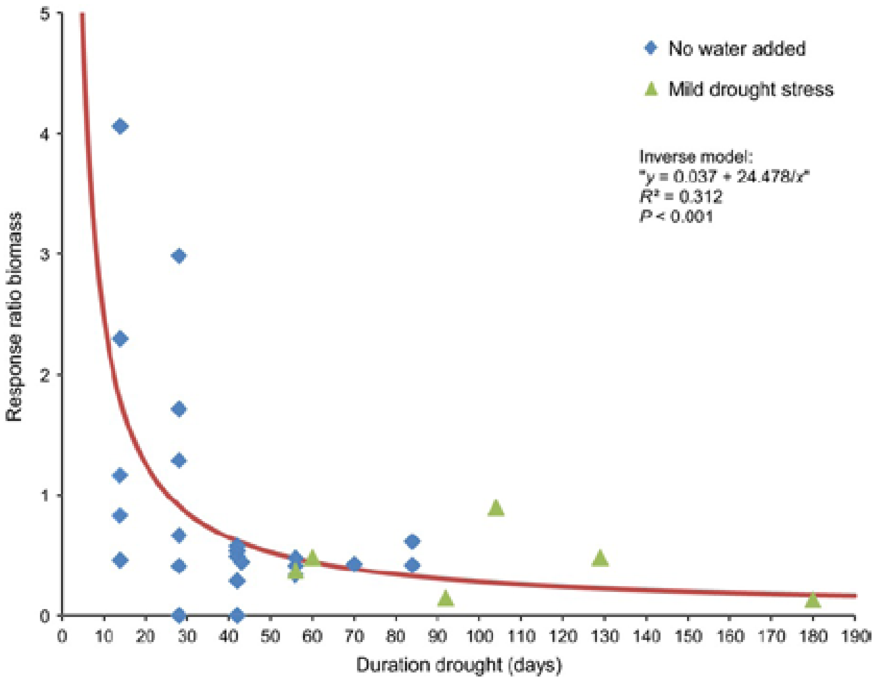
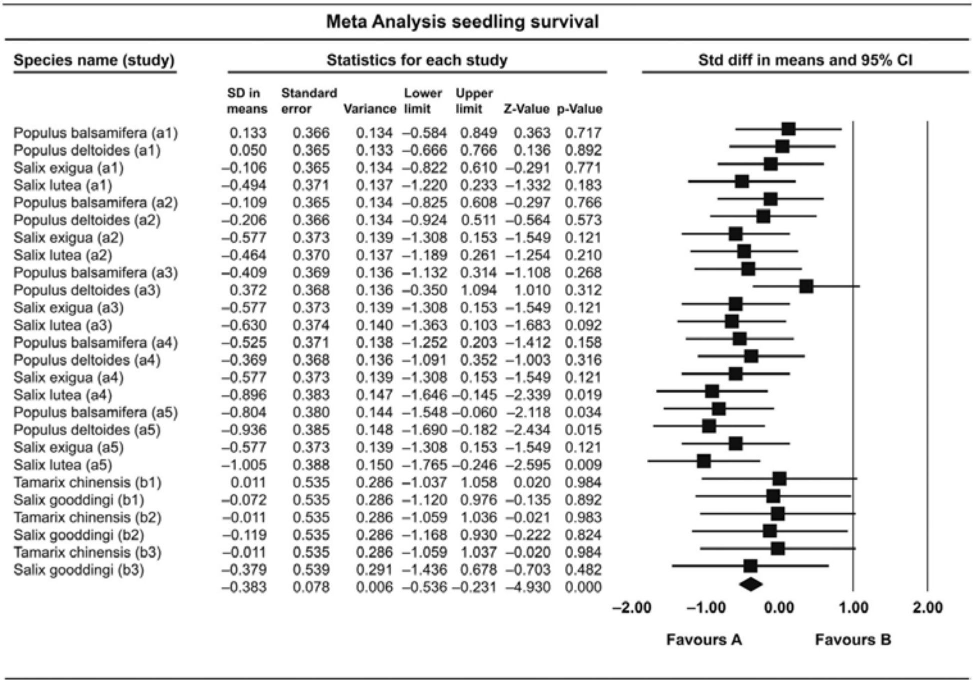


Fig. 2.1. Effects of duration of drought on riparian plant biomass ratio (mean biomass in drought treatment/ mean biomass in control). Studies with intense drought conditions (no water added, or the plants were not watered until the wilting point was reached) and mild drought conditions (water periodically withheld) are indicated by different symbols. A weighted regression analysis is shown. n = 31 cases, from 12 studies.

Seedling survival

The studies concerning seedling survival differed in their degree of drought intensity from very mild drought stress (1 cm water table decline per day) to more severe drought stress (8 cm water table decline per day). The duration of the drought periods ranged from 3 to 90 days. Our meta-analysis confirms the general picture that drought overall has a strong negative effect on seedling survival (Table 2.2; $P < 0.001$). Regression analyses on all available cases show a pronounced negative linear response of seedling survival to an increase in the duration of drought (Fig. 2.2a). The negative effect becomes really strong in the case of droughts lasting longer than approximately 30–35 days. When seedling survival is plotted against the duration of drought multiplied by drought intensity (water decline ranging from 1 to 8 cm per day), an even clearer linear effect of drought on seedling survival becomes visible (Fig. 2.2b). Both linear relationships are strong, but show a wide variation among the data points, with no clear cut-off point indicating where response ratios drop below 1.

Table 2.2. Outcome of random-effects model meta-analysis on effects of drought on seedling survival. Standard differences (SD) in means with a negative value ('Favours A') indicate a negative effect of drought on survival in the respective study, while positive values ('Favours B') indicate a positive effect. For two of five studies, including 26 cases, the P-values could be calculated. The three other studies did not show standard deviations or statistical output; hence, meta-analysis results could not be calculated for these studies. Source studies are as follows, identified by letters in parentheses. Type of study: greenhouse experiments, except Stella et al. (2010) who performed a mesocosm experiment. Amlin & Rood, 2002 (a); Horton & Clark, 2000 (b); Mahoney & Rood, 1991; Stella et al., 2010; Van Splunder et al.,1996. See reference section for complete references.



Meta Analysis seedling survival

Species name (study)	Statistics for each study						
	SD in means	Standard error	Variance	Lower limit	Upper limit	Z-Value	p-Value
Populus balsamifera (a1)	0.133	0.366	0.134	–0.584	0.849	0.363	0.717
Populus deltoides (a1)	0.050	0.365	0.133	–0.666	0.766	0.136	0.892
Salix exigua (a1)	–0.106	0.365	0.134	–0.822	0.610	–0.291	0.771
Salix lutea (a1)	–0.494	0.371	0.137	–1.220	0.233	–1.332	0.183
Populus balsamifera (a2)	–0.109	0.365	0.134	–0.825	0.608	–0.297	0.766
Populus deltoides (a2)	–0.206	0.366	0.134	–0.924	0.511	–0.564	0.573
Salix exigua (a2)	–0.577	0.373	0.139	–1.308	0.153	–1.549	0.121
Salix lutea (a2)	–0.464	0.370	0.137	–1.189	0.261	–1.254	0.210
Populus balsamifera (a3)	–0.409	0.369	0.136	–1.132	0.314	–1.108	0.268
Populus deltoides (a3)	0.372	0.368	0.136	–0.350	1.094	1.010	0.312
Salix exigua (a3)	–0.577	0.373	0.139	–1.308	0.153	–1.549	0.121
Salix lutea (a3)	–0.630	0.374	0.140	–1.363	0.103	–1.683	0.092
Populus balsamifera (a4)	–0.525	0.371	0.138	–1.252	0.203	–1.412	0.158
Populus deltoides (a4)	–0.369	0.368	0.136	–1.091	0.352	–1.003	0.316
Salix exigua (a4)	–0.577	0.373	0.139	–1.308	0.153	–1.549	0.121
Salix lutea (a4)	–0.896	0.383	0.147	–1.646	–0.145	–2.339	0.019
Populus balsamifera (a5)	–0.804	0.380	0.144	–1.548	–0.060	–2.118	0.034
Populus deltoides (a5)	–0.936	0.385	0.148	–1.690	–0.182	–2.434	0.015
Salix exigua (a5)	–0.577	0.373	0.139	–1.308	0.153	–1.549	0.121
Salix lutea (a5)	–1.005	0.388	0.150	–1.765	–0.246	–2.595	0.009
Tamarix chinensis (b1)	0.011	0.535	0.286	–1.037	1.058	0.020	0.984
Salix gooddingi (b1)	–0.072	0.535	0.286	–1.120	0.976	–0.135	0.892
Tamarix chinensis (b2)	–0.011	0.535	0.286	–1.059	1.036	–0.021	0.983
Salix gooddingi (b2)	–0.119	0.535	0.286	–1.168	0.930	–0.222	0.824
Tamarix chinensis (b3)	–0.011	0.535	0.286	–1.059	1.037	–0.020	0.984
Salix gooddingi (b3)	–0.379	0.539	0.291	–1.436	0.678	–0.703	0.482
	–0.383	0.078	0.006	–0.536	–0.231	–4.930	0.000

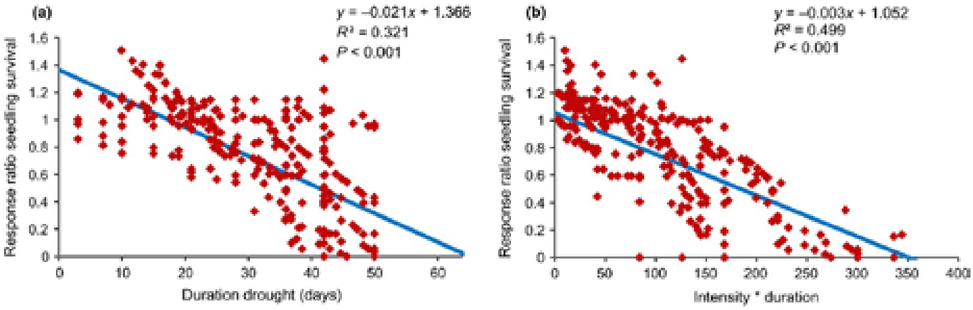


Fig. 2.2. Riparian seedling survival (mean number of seedlings treatment/seedlings control) in relation to (a) the duration of drought and (b) the intensity of drought (cm water decline per day) * duration (days of drought). Weighted regression analyses are shown. (a) n = 261, from five studies. (b) n = 257, from five studies.

The response ratio of seedling survival in relation to the water table decline per day gives a clear picture of the effect of drought intensity (Fig. 2.3). The cases with a 1–2 cm water table decline per day reveal a relatively mild negative relationship, which is almost significant. A decline of 3–4 cm per day shows a significant negative relationship with a steeper slope and a decline of 6–8 cm per day results in an even stronger negative relationship with the response ratio of seedling survival. All selected studies on seedling survival reported data on tree seedlings of the genera *Populus, Salix* and *Tamarix*. If we look at these genera specifically, response ratios of the survival of seedlings of both *Populus* and *Salix* show a negative relationship with drought duration, while seedling survival of *Tamarix* does not show a significant trend and seems hardly affected by drought. The general response of *Salix* seedling survival is smaller than for *Populus*. Hence, differences in seedling drought tolerance between these three common riparian tree genera are large (Fig. 2.4).

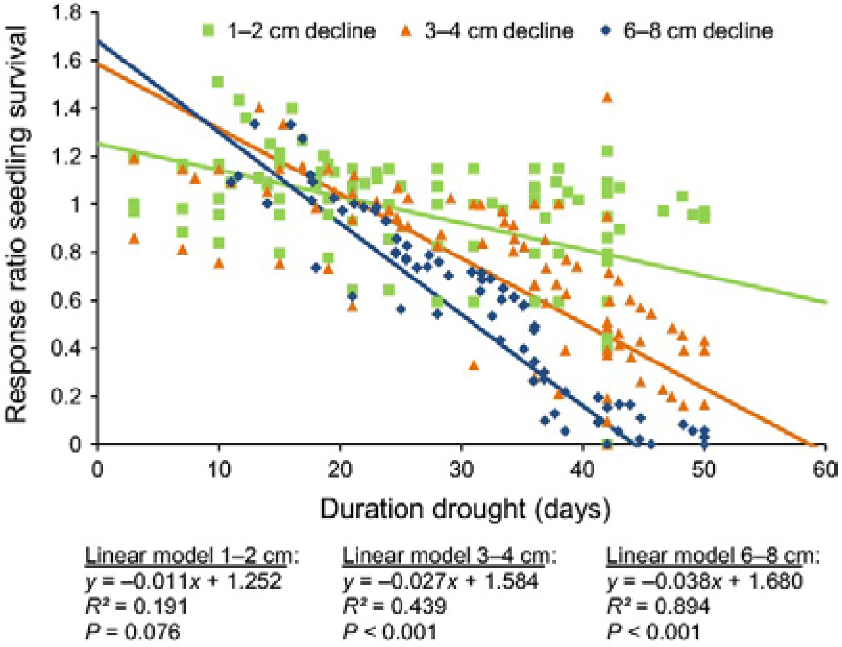


Fig. 2.3. Effects of duration of drought on the response ratio of riparian tree seedling survival (mean number of seedlings treatment/seedlings control), with different declines of water table per day (1–2 cm, 3–4 cm and 6–8 water). Weighted regression analyses are shown. n = 257 from five studies. All data points are related to the riparian tree genera *Populus*, *Salix* and *Tamarix* (comparable data points are shown in Fig. 2.4).

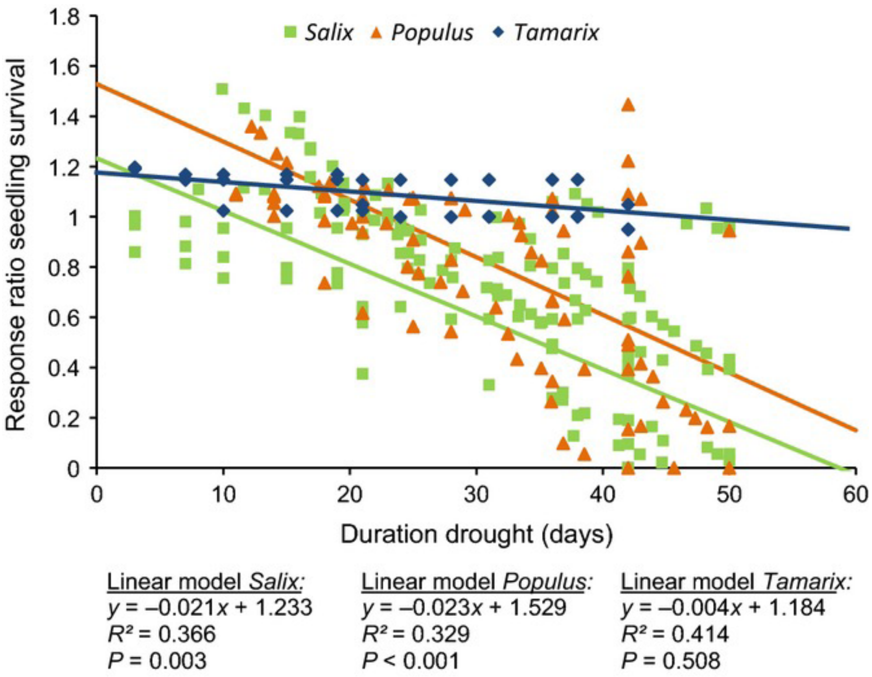


Fig. 2.4. Effects of duration of drought on seedling survival (mean number of seedlings treatment/seedlings control) of the genera *Populus*, *Salix* and *Tamarix.* All data points related to each genus are indicated. Weighted regression analyses are shown. n = 261 from five studies.

Three studies (Mahoney & Rood, 1991; Van Splunder et al., 1996; Horton & Clark, 2000) totalling 14 cases contained quantitative data on the response of root length of seedlings to drought conditions. In these studies, the authors emphasised that species' ability to increase root length is important for tolerating drought conditions. The genera *Salix* and *Populus* had on average a lower response ratio of the root length as a reaction to drought (response ratio of 1.27 and 1.53, respectively), compared with the genus *Tamarix* (response ratio of 2.02). This difference between species of the three common riparian tree genera in root elongating ability most likely explains their capacity to survive increased periods of drought as seedlings. Furthermore, we explored the effects of drought duration on plant height, but found no clear trend.

Species richness

The main findings of 11 selected studies considering drought effects on riparian plant species diversity are described individually (see Table S2.2). Shifts in species composition and a decrease in riparian species richness were found in almost all studies as a result of periods of more intense, or prolonged summer drought. A decline in riparian plant species richness was found in nine of 11 studies, as a result of a prolonged drought period or increased drought intensity. The studies conducted in desert systems provided quantitative data; water tables ranged from about 4 to 20 m below the ground surface, and stream flow permanence ranged from 71 to <25% in these drought-affected sites. Several studies showed a decline of herbaceous or woody species only (two and three species respectively), whereas other species found declines in both plant categories (four studies). Seven of 11 studies found a shift in species composition from hydric to mesic or xeric species going from the channel upwards, with a relatively high abundance of mesic and xeric species in drought-affected riparian zones. Groundwater table and surface flow permanence are regarded as the main abiotic factors underlying the degree of change in species richness. Plant traits, especially rooting depth and water use efficiency, are mentioned to be important for species to survive dry spells. A strong water table decline, a decrease or absence of surface water flow, in combination with the presence of species with a lack of adaptation to drought, are mentioned to negatively affect species richness. In the articles focussing on dry land or semi-arid systems (six out of 11 articles), surface flow permanence was mentioned to be one of the most important regulating factors for maintaining species diversity (Lite & Stromberg, 2005; Stromberg et al., 2005, 2007; Salinas & Casas, 2007; Stromberg et al., 2009; Stromberg et al., 2010). In Arizona's Sonoran Desert region for example, streams with flow permanence of <25% have significantly lower riparian species diversity than streams with higher flow permanence (Stromberg et al., 2007). Riparian plant species richness was mentioned to be dependent on groundwater depth in eight of 11 studies.

While the above-mentioned studies all dealt with an increase in drought and a reduction in groundwater tables and soil moisture at the drier end of the riparian zone, one study in the Boreal region (Ström et al., 2011), focussed on the impact of a reduction in flooding at the wetter end of the riparian zone. Their study demonstrated that a reduction in summer flooding duration positively affects species richness. This increase in species richness was mainly related to a decrease in biomass of two dominant species: *Carex canescens* and *Carex acuta*. This particular study demonstrates that in Boreal continental-climate regions, reduction in summer flooding may increase local species richness at the wetter (lower) end of the riparian zone, while summer drought reduces the width of the riparian zone and its species richness in general.

Hydrological thresholds

Only a few studies that evaluated species responses to drought identified hydrological thresholds for changes in species composition. Lite & Stromberg (2005) clearly indicate that the riparian species *Populus fremontii* and *Salix gooddingii* were dominant over *Tamarix ramosissima* at sites where surface flow was present more than 76% of the time, inter-annual groundwater fluctuation was <0.5 m, and average maximum depth to groundwater was <2.6 m. In this system along the San Pedro river in Arizona, stream flow permanence ranged from 29 to 100%, and maximum depth to groundwater fluctuated from 5.3 to 1.3 m. For each system, there are individual values for ranges in water table fluctuations, which determine the vegetation composition and species responses (see Table S2.2, final column). While we summarised all available information on (potential) hydrological thresholds, our review analysis clearly shows that the presented values are study specific thresholds, which are hard to generalise, since they are system specific. This demonstrates that, while badly needed to help estimate future effects, there is currently no general framework for hydrological thresholds, to indicate when changes in riparian species composition occur. However, the results derived from our meta-analysis, indicate that a drought period lasting longer than approximately 30–35 days, combined with a strong drought intensity (a 3–4 cm water table decline per day or more) can have a detrimental effect on both biomass and seedling survival.

Discussion

Our meta-analysis confirms that a longer duration and greater intensity of drought negatively affect both riparian plant total biomass (dry weight) and seedling survival, starting from a drought duration of approximately 30–35 days, although an exact critical threshold is hard to determine. A detailed analysis of the intensity effect shows that seedling mortality clearly increases with a more rapid desiccation of the habitat (starting from a decline in water table of 3–4 cm per day). The differences found between seedlings of three common riparian tree genera are consistent with their general habitat preferences, with both *Populus* and *Salix* showing a negative relationship of survival in response to increasing duration of drought, while *Tamarix* is hardly affected. *Tamarix* seedlings can cope relatively well with drought conditions, mainly due to their ability to rapidly and expansively elongate their roots. The declines in biomass and seedling survival due to increased drought duration and intensity are expected to lead to a high species turnover, thereby affecting species composition. Plant communities are expected to change towards more drought-tolerant species. Indeed, our review shows that an increase in the duration and intensity of drought generally results in an eventual decline in riparian plant species richness, due to plant mortality, and a shift in species composition from hydric species to mesic and/ or xeric species. According to this shift, the riparian zone with hydric species is reduced or narrowed, and part of it is replaced by a zone with mesic or even xeric terrestrial species. While dispersal limits plant species colonisation, and hence replacement rates in riparian zones (Brederveld et al., 2011), the rapid replacement of riparian wetland species by mesic or xeric terrestrial species is likely facilitated by the latter species having nearby source populations in the uplands adjacent to the riparian zone.

We have to stress here that, in addition to an increase in the duration and intensity of drought, climate change is also expected to lead to prolonged or more intense periods of increased flooding (IPCC, 2007; Bates et al., 2008). Therefore, in future riparian plants may have to show a combination of improved tolerance to drought and flooding, to survive. Also, abiotic factors that affect riparian plant communities, such as changes in nutrient availability and soil type, are important to consider, as well as interaction effects between different drivers of riparian plant dynamics.

Species vary extensively in their internal mechanisms to limit mortality and thereby tolerate drought. Herbaceous species generally are more sensitive to subsurface moisture and less to groundwater table decline compared with tree species (Higler, 1993). For this reason, it can be expected that herbaceous species show more sensitivity to the direct effects of rainfall declines, while tree species are more sensitive to prolonged, more severe stream discharge declines, which also affect groundwater tables. This may lead to a decline in herbaceous species in the short term, and a decrease in tree species in the long run due to an increase in mortality and reduction in seedling recruitment. Groundwater level, surface flow permanence and the presence of plant traits conducive to drought tolerance, most notably plasticity in root elongation, were mentioned as the most important factors determining the changes in species richness and composition. These results were found across (semi-) arid, Atlantic and Mediterranean systems. The time-scale of changes in species richness differs between these systems, with a drought impact on species richness already occurring during dry seasons in (semi-)arid systems (Lite & Stromberg, 2005; Stromberg et al., 2005, 2007, 2009) and a more gradual response in more temperate regions, where changes in species richness may take several to many years. Full adjustments of plant communities to a new hydrological regime can take more than 10 years in Boreal systems (Ström et al., 2011). In the warm Mediterranean area of Western Australia, a progressive change in riparian community composition towards drought-tolerant riparian species was observed under water table drawdown rates of 9 cm per year over a 33-year period (Froend & Sommer, 2010). Climate models predict the most profound increase in drought frequency and duration to take place in areas where droughts already regularly occur; examples are southern Europe and the Middle-East (Dai, 2011). The most abrupt changes in plant communities are to be expected for regions that are influenced most severely by intense drought events. However, sites that were historically less affected by drought might be adapted to a lesser degree to such conditions, so that extreme summer drought events may have more pronounced effects on riparian plant communities there. Our meta-analysis confirms that the longer a drought lasts, the stronger will be its negative effect on riparian plant biomass and seedling survival, mainly triggered by critical levels of soil water potential for the respective species. A relatively long drought period leads to water stress and the closure of the plants' stomata, to save water from evaporation (Amlin & Rood, 2002). Closed stomata will in turn lead to reduced CO_2 availability and consequently reduced photosynthetic activity, which will lead to an extra reduction in water use (Elcan & Pezeshki, 2002). The differences among plant species in seedling survival can be explained by several underlying traits. Root elongation of the seedling is an important factor mentioned in four of five studies explaining the decrease in seedling survival due to drought. Reduction in plant height and leaf area is also mentioned as important factors in the majority of studies (three of five studies), reducing the transpiration area of the plant and thereby saving water. In general, *Salix* was slightly more sensitive to drought than *Populus* along (semi)-arid or Mediterranean streams (Van Splunder et al., 1996; Amlin & Rood, 2002; Stella et al., 2010). According to Amlin & Rood (2002), these differences in seedling responses might be caused by the smaller seed size and correspondingly reduced respiratory reserves of *Salix* seedlings, leading to a slower growth of willow seedling roots compared with cottonwood roots. As a consequence, the willow seedlings were not able to maintain contact with the receding water table and capillary fringe, and hence survival decreased. The natural niches are also important to consider here; *Salix* often grows closer to the stream than *Populus,* which usually grows at higher locations. Seedlings of the species *Tamarix chinensis* are hardly susceptible to drought (Horton & Clark, 2000; Lite & Stromberg, 2005; Salinas & Casas, 2007; Stromberg et al., 2007, 2010). Increased drought periods in semi-arid or Mediterranean systems and the invasive character of *Tamarix* spp. and its specific response mechanisms to cope with drought may lead to a further domination of *Tamarix* over *Salix* and *Populus* spp. and other typical riparian species in the near future.

To help predict effects of future increased summer drought on riparian vegetation, a general framework for hydrological thresholds is needed. These threshold values may consist of critical values for groundwater or surface water levels at which riparian species composition may shift. Since riparian wetlands are dynamic and heterogeneous systems, we suggest that for a general framework the riparian zone should be divided into subzones with different flooding frequencies and groundwater levels for which critical threshold values are determined. Increasing summer drought may initially result in species from drier parts of the riparian zone moving 'downslope', with the riparian zone itself narrowing at the upper end. Thresholds, especially for the replacement of wetland species by more common terrestrial species, are critical especially for this upper end. Our results emphasise that a classification into different systems should be made to find such thresholds, based on the biogeographic regions, such as Boreal, Atlantic and Mediterranean systems. A further relevant distinction between systems can be made based on their flow permanence; perennial streams (continuous flow), intermittent streams (absence of flow during a few weeks or months) and ephemeral streams (flow only for hours or days following heavy rainfall). The use of plant functional groups, based on the species' flow response guilds (Merritt et al., 2010), is recommended to allow a generalisation for species responses to changes in hydrological factors. Our meta-analysis on biomass and seedling survival studies makes it possible to identify a drought duration threshold: a drought lasting longer than 30–35 days poses a high risk of detrimental effects on both riparian plant biomass as well as riparian tree seedling survival (results related to the genera *Salix*, *Populus* and *Tamarix*). The latter is especially the case for high drought intensities (starting from 3 to 4 cm water table decline per day). These thresholds give important indications to improve water management to reduce the risks for riparian species during periods of drought.

Our meta-analysis included cases with a study design considering a decline in water table, thereby excluding the primary effects of a temperature increase. In most natural cases, summer drought is stimulated by a temperature increase, as well as decreasing precipitation. An increase in temperature without drought effects is expected to stimulate growth, biomass accumulation and reproduction. Increased temperature in combination with reduced precipitation and thereby increased evaporation will lead to reduced soil moisture and declining groundwater tables. This may lead to a very strong decline in biomass and seedling survival, and, in the long-run, decline in species richness. Further research on the interactive effects of climate-driven changes in temperature and hydrology on riparian plant communities would be useful to help estimate effects of both.

Acknowledgments

This work was supported by the European Union 7th Framework Project REFRESH under contract no. 244121.

Supporting information

Table S2.1. Key word strings used for the literature search, with results.

Subq. 1: Summer drought effects on riparian plant species richness

- “drought” AND (“species richness” OR “species number” OR “species abundance” OR “species diversity”) AND (“plant*” OR “vegetation”) → 357 articles → refined with “ripar*” OR “wetland*” OR “stream*” OR “river*” OR “floodpl*”→ 62 articles (1)

- “climate change” AND (“species richness” OR “species number” OR “species abundance” OR “species diversity”) AND (“plant*” OR “vegetation”) → 759 articles → refined with “ripar*” OR “wetland*” OR “stream*” OR “river*” OR “floodpl*”→ 71 articles (2)

Subq. 2: Summer drought effects on biomass production

- “drought” AND “biomass*” AND (“plant*” OR “vegetation”) → 2241 articles → refined with “ripar*” OR “wetland*” OR “stream*” OR “river*” OR “floodpl*”→120 articles (1)

- “climate change” AND “biomass” AND (“plant*” OR “vegetation”) → 1856 articles → refined with “ripar*” OR “wetland*” OR “stream*” OR “river*” OR “floodpl*”→ 151 articles (2)

Subq. 3: Summer drought effects on seedling survival

- “drought” AND “seed*” AND (“plant*” OR “vegetation”) → 4991 articles → refined with “ripar*” OR “wetland*” OR “stream*” OR “river*” OR “floodpl*”→ 182 articles (1)

- “climate change” AND “seed*” AND (“plant*” OR “vegetation”) → 1244 articles → refined with “ripar*” OR “wetland*” OR “stream*” OR “river*” OR “floodpl*”→ 90 articles (2)

- “drought” AND “seedling*” AND ”survival” AND (“plant*” OR “vegetation”) → 594 articles → refined with “ripar*” OR “wetland*” OR “stream*” OR “river*” OR “floodpl*”→ 42 articles (3)

- “climate change” AND “seedling*” AND ”survival” AND (“plant*” OR “vegetation”) → 111 articles → refined with “ripar*” OR “wetland*” OR “stream*” OR “river*” OR “floodpl*”→ 10 articles (4)

Table S2.2. Summary of the main effects of drought on riparian plant species richness and composition, organized according to the main trends in species declines.

Authors	Main trend	Main observations	Mechanisms	Bio-geographical region	Research set-up	Thresholds or indicator species
Stromberg *et al.,* 2005	Decline of herbaceous species.	During early summer drought, streamside herbaceous cover and species richness declined across spatial gradients of decreased flow permanence. Composition shifted from hydric to mesic species at sites with more intermittent flow.	Depth to groundwater table, perennial stream flows and high soil moisture are important to sustain hydric species.	Desert	Comparison between sites with perennial and ephemeral stream flow. May - August 2000 - 2003.	Hydrologic threshold values evident for one plant functional group: *Schoenoplectus acutus. Juncus torreyi*, and other hydric riparian plants declined sharply in cover with loss of perennial stream flow.
Westwood *et al.,* 2006	Decline of herbaceous species.	Prolonged periods of channel desiccation and steep channel gradients lead to a decline in species diversity and an increase in non-aquatic grasses and herbs. High local water stages and wide channels lead to an increase in species diversity.	Steep channel gradients (≥ 4 m km^{-1}) and narrow channels (≤2 m width) have a negative effect on species richness (correlation diversity with local slope is -0,302).	Atlantic	Post-drought monitoring (1992-1995) and recurrence of drought conditions (1996-1998).	The macrophyte *Ranunculus peltatus* has an important indicator value for its ability to withstand drought, compared to *R. penicillatus*.
Tabacchi, 1995	Increase of short-lived and exotic species (pioneers).	Overall, richness and density of exotic species were greatly increased following warm or dry periods. Plots adjacent to active river channels showed greatest sensitivity to drought conditions. Here, the density of short-lived and exotic species increased.	There is a high variation in mean daily discharge between a normal year, a wet year, and a dry year.	Atlantic	Pioneer vegetation, changes in space and time measured. Normal (1987), wet (1988) and a dry year (1989).	Plots adjacent to active river channels showed greater sensitivity to drought conditions.
Jansson *et al.*, 2007	Decline of both woody and herbaceous species.	Groundwater discharge areas in riparian zones were 36 - 209% more species rich than non-discharge areas.	Drought stress and low nitrogen availability are suggested as the major causes for a decrease in species diversity.	Atlantic	Groundwater discharge versus non-discharge areas.	Riparian species growing in high elevations more often subject to drought stress during low-river stages than low-elevation aquatic species.

Salinas & Casas, 2007	Decline of both woody and herbaceous species.	At intermittent and highly drought impacted sites, hydric or mesic species declined or disappeared, leaving communities dominated by drought-tolerant / xeric species. Decline of woody sp. richness with shorter hydroperiod.	Decline in rainfall coupled with higher temperatures and evaporative stress at lower elevation open-canopy sites may have constrained herbaceous species. Surface flow permanence was a limiting factor for woody riparian vegetation.	Mediter.	Responses of vegetation to main environmental gradient investigated during 2 years.	Increase in abundance of *Tamarix africana* accompanied by halotolerant shrubs or emergent macrophytes in sites that were affected by drought.
Stromberg *et al.*, 2007	Decline of both woody and herbaceous species.	As stream flow becomes intermittent and groundwater deepens, diversity and cover of herbaceous species along the low-flow channel decline. Species composition shifts from wetland pioneers (*Populus, Salix* spp.) to more drought-tolerant shrub species (*Tamarix, Bebbia* spp.).	Depth to groundwater, intra- and inter-annual fluctuations in water table level and groundwater decline rate influence the riparian vegetation. A stream flow permanence of <25% corresponds with the lowest species diversity. Groundwater depth during drought can be >4m at intermittent sites, with intra-annual variation of >1 m, compared with mean depths of <2 m and intra-annual fluctuation of <0.3 m at some perennial sites.	Desert	Year-round survey of several reference rivers in Arizona's Sonoran Desert region.	As groundwater deepens species composition shifts from wetland pioneers (*Populus, Salix*) to more drought-tolerant shrub species (*Tamarix, Bebbia*). Shallow-rooted wetland herbaceous plants respond fast to declines in stream flow and groundwater depth.
Lite & Stromberg, 2005	Decline of (pioneer) tree and shrub species.	*Tamarix ramosissima* can tolerate a wider range of ground-water fluctuations and depths than *Populus fremontii* and *Salix gooddingii.*	Surface flow permanence and groundwater depth, in relation to plant rooting depth and water use efficiency. Stream flow permanence ranged from 29-100%, max. depth to groundwater from 5.3 to 1.3m, and from 1.5 to 0.05m in max. groundwater fluctuation (Jan-Jun).	Desert	Dry sites, as representative of future dewatered conditions, were compared to sites less affected by drought. Two year survey.	*Populus fremontii* and *Salix gooddingii* were dominant over *Tamarix ramosissima* at sites where surface flow was present more than 76% of the time, inter-annual ground-water fluctuation was <0.5 m, and average maximum depth to ground water was <2.6 m.

Table S2.2. *Continued*

Authors	**Main trend**	**Main observations**	**Mechanisms**	**Bio-geographical region**	**Research set-up**	**Thresholds or indicator species**
Stromberg *et al.*, 2009	Decline of (pioneer) tree and shrub species.	Species richness in the riparian zone with ephemeral-flow was lower during a drought season compared to the more permanent water sources of the perennial-flow sites. Mesic, annual and herbaceous perennial species more diverse at perennial-flow sites than ephemeral-sites during drought.	Diversity in dry land regions is frequently limited by surface and groundwater. At ephemeral-flow study sites surface flow present only after major storm events, depth to groundwater about 20 m below ground surface. At perennial-flow study sites depth to groundwater from about 1-5 m below ground surface.	Desert	Comparison between sites with perennial stream flow and ephemeral stream flow over a 2 year period spanning drought and wetter conditions.	Higher relative abundance of xeric species during drought.
Stromberg *et al.*, 2010	Decline of (pioneer) tree and shrub species.	Field data indicate that increased drought conditions cause the floodplain plant community to shift from hydric pioneer trees and shrubs towards mesic species.	Stream flow permanence was a determinant factor and ranged from 29-71% at the dry sites compared to the wet sites, where flow permanence ranged from 79-100%. Mean depth to ground water table ranged from about 5 -1 m.	Desert	Comparison between sites differing in degree of stream intermittency and flood intensity. Experiment was conducted for 2 years.	*Tamarix* species are very tolerant to drought. Plant traits and adaptations to drought are important, especially long rooting depth of the mesic species.
Ström *et al.*, 2011	Increase in species richness, shift in species composition.	Riparian vegetation from the lowest end transplanted to higher elevation decreased in biomass and increased in species richness. Climate-driven hydrologic changes will stimulate the replacement of riparian plant communities by terrestrial comm. at the top, resulting in narrower riparian zones.	Flood duration played a strong role for structuring riparian plant community organisation. The low elevation in the riparian zone was flooded on average 37.4 days per year, while the mid elevation was flooded on average 6.9 days, and the high elevation 1.7 days per year.	Boreal	Transplantation experiment with turfs transplanted higher up the floodplain to simulate drought conditions, monitored over 6 years.	*Carex canescens* and *C. acuta* remained high in frequency at high elevations, but decreased in biomass production, potentially as a result of drought stress. Biomass response to new hydrological regimes is rather quick (one season to the next), while overall community adjustments in species composition take much longer.

Chapter 3

Effects of increased summer drought on riparian plant community diversity and functioning: a comparative study along a European climate gradient

Annemarie G. Garssen, Liliana García, Edwin T. Pos, Annette Baattrup-Pedersen,
Carl C. Hoffman, Isabel Pardo, Jos T.A. Verhoeven and Merel B. Soons

Abstract

Periods of summer droughts occur more frequently in many parts of the world, with substantial anticipated effects on riparian plant community composition and species richness. Stream riparian zones are in general rain-fed systems and therefore sensitive to increased drought episodes. We conducted a comparative study in Atlantic Europe and experimentally modified the hydrology of five streams across three countries (Denmark, the Netherlands and Atlantic Spain) during summer (end of June to September) over a period of 3 years. We assessed the responses in riparian plant species richness, Shannon diversity, biomass, plant-available nitrogen and phosphorus to decreased water tables.

Our results demonstrated that a drought duration of approximately 10 weeks with an average reduction of water tables by ca. 10 cm had a small impact on the stream riparian vegetation. Only in the third, final year of the experiments, there was a clear trend of a lower species richness at the drought treatment sites compared to the control sites. When considering all years, we found a significant increase in extractable soil N and a decrease in biomass with declining water tables. It is expected that severe drought periods where low stream water tables are combined with very limited rainfall, resulting in streambeds that dry out to a greater extent, will have a more severe impact on riparian vegetation compared to our experiment. Robust riparian zones with sufficient space and a natural hydrological gradient are important for preserving the high plant species diversity characteristic for these ecosystems in a changing climate.

Introduction

Worldwide, more frequent hot and fewer cold temperature extremes are predicted to occur (IPCC 2013). This warmer and more variable climate is predicted to enhance the likelihood of extreme weather events such as droughts and floods (Wetherald & Manabe, 2002). In Central Europe and the Mediterranean area, summer droughts are likely to increase in frequency of occurrence (Christensen et al., 2007; Feyen & Dankers, 2009) due to a decrease in precipitation combined with an increase in evaporation in spring and summer (Douville et al., 2002; Wang et al., 2005). Especially in Southern Europe extremely dry and warm summers are expected to occur in the near future (IPCC, 2013).

These more frequent and longer dry periods are expected to have significant impacts on lowland streams and their adjacent riparian wetland zones (Arnell & Reynard, 1995; IPCC, 2007; Dankers & Feyen, 2009). These systems are sensitive to drought, because they are in general rain-fed systems (Décamps, 1993). By the end of this century, droughts affecting stream water flows are estimated to increase by up to

40-75% in most of Europe in the frost-free season (Feyen & Dankers 2009) and this is likely to particularly impact lowland streams.

Riparian plant communities along lowland streams may respond to increased drought by shifts in species composition or changes in species' phenology or characteristics (Hughes, 2000; Parmesan, 2006; Thuiller, 2005). First, species may undergo range shifts across the hydrological gradient due to unfavourable conditions during drought associated with changes in moisture availability. Both a decline of riparian species richness and a shift towards species adjusted to drier conditions may be the result of increased periods of drought, with a shift from hydric to mesic or even xeric species in strongly drought-affected riparian zones (Garssen et al., 2014). Secondly, drought may affect individual plant responses. The duration and intensity of the drought period, as well as the presence of plant species with specific traits, influence the responses of riparian vegetation to drought conditions (Baattrup-Pedersen et al. 2018; Garssen et al., 2014). Several response mechanisms associated with drought conditions can be shown by individual plant species, such as the maintenance of a favourable internal water content, an increase in water use efficiency (Kozlowski & Pallardy, 2002), an increase in rooting depth (increasing water uptake) and/or a decrease in above-ground biomass (reducing water loss) (Liu et al*.,* 2005; Ström et al., 2011).

Hydrological shifts such as a higher frequency of extreme droughts, are likely to involve species shifts and changes in the relative abundance of functional plant traits associated with the ability to efficiently use and/or conserve water (Baattrup-Pedersen et al., 2018). This implies that the vegetation will show changes in functional composition with respect to water-conserving traits such as low specific leaf area (SLA) (Poorter & Markesteijn, 2008; Douma et al., 2012). In a recent study, the effects of drought on taxonomic diversity and functional trait composition of riparian vegetation showed a large variation, likely caused by local differences in abiotic conditions among study sites. The decline in functional diversity in response to drought was most prominent near the streams (Baattrup-Pedersen et al., 2018). In addition, a meta-analysis has shown that a drought duration of more than 30 to 35 days, combined with high drought intensities (3 to 4 cm water table decline per day or more) under experimental conditions strongly reduces riparian plant biomass and riparian seedling survival (Garssen et al., 2014). Strong water table declines, a decrease or absence of surface water flow, in combination with the presence of species with a lack of adaptation to drought were mentioned most frequently as factors determining riparian plant species responses in the scientific literature (Garssen et al., 2014).

While experimental studies have addressed plant responses to drought under controlled conditions, it remains unclear how drought treatments alter riparian communities in the field. Therefore, it was our objective to investigate the effects of increased drought conditions on entire riparian plant communities under natural conditions. We carried out a field experiment to study the effects of drought by lowering stream water levels during summer. This experiment was conducted at five different European lowland streams along a climatic gradient across Atlantic Europe from Denmark to Spain. Our goals were to: (1) investigate the overall responses in riparian plant species richness, biomass, and plant-available N and P to increased drought conditions, and (2) explore if the drought experiment, conducted during a three-year period, leads to more variation in species and a different vegetation composition between treatments in the investigated European lowland streams.

Materials and methods

Five European riparian areas, ranging from Denmark (2 sites), to the Netherlands (1 site) and Spain (2 sites) were selected for the drought experiment. In Denmark, the experimental riparian areas were situated along a channelized agricultural stream (Voel bæk, Fig. 3.1a) and a more pristine forest stream (Sandemandsbækken, Fig. 3.1b). In the Netherlands, the riparian area was situated along an agricultural stream of which the riparian zone had been partly restored (Groote Molenbeek, Fig. 3.1c). In Spain, more pristine riparian areas along partly forested lowland streams were selected for the field experiment (Pego, Fig. 3.1d; Caselas, Fig. 3.1e).

The experimental areas were laid out in the riparian zones stretching over a length of approximately 150 m along each stream. A control and drought treatment with similar plant communities were selected within this riparian zone. We constructed a side channel or longitudinal dam to convert the water at each drought treatment and create a significantly lower surface water table in the treatment stream section than under normal summer conditions. In the control sections, stream water tables were not manipulated. The drought experiments were conducted during three consecutive years in Denmark and the Netherlands (2011-2013) and during one year in Spain (2012). The manipulated drought period lasted approximately 10 weeks each year within the period from end of June to September.

Within each treatment three transects perpendicular to the stream were selected along the stream riparian gradient (SRG), ranging from the lowest water table 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 along each transect. The choice of these points was based on records of recent water levels and expert judgment of involved researchers and stakeholders from water boards. Sampling points 1 were situated closest to the stream, just above the normal summer water table. These points are normally not inundated in summer, but inundated during normal winter floods. Sampling points 2 were situated just above the normal winter water table, so that they are normally not flooded in summer or winter. Sampling points 3 were situated at

Figure 3.1. Overview of the stream riparian wetland sites in Atlantic Europe (a) with pictures of the drought treatments: Sandemandsbækken (Denmark) (b), Voel bæk (Denmark) (c), Groote Molenbeek (the Netherlands) (d), Pego (Spain) (e), Caselas (Spain) (f).

Measurements

During each manipulated drought period, water tables at all sampling points were continuously monitored in piezometers with a full screen length, using a Diver® and by manual measurements, using a sounding device every two weeks until the final stage of the experiment. Ammonium, N and P in the water samples were measured according to European standard methods (EN ISO 11732; EN ISO 13395; EN ISO 6878, respectively). Each year, close to the end of the drought experiment (mid-August), potential plant available nutrients were determined from three pooled soil cores of the top ten 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, Colorado, USA; APHA 2005). Extractions with 0.5 M sodium carbonate were carried out to determine extractable soil P (Olsen et al., 1954).

During summers, plant above-ground biomass at the sampling points was clipped at peak standing crop (August), oven-dried (48 h, 70 °C) and weighed. Vegetation relevées were made during the growing season (June - September). Species composition was recorded according to the Braun-Blanquet method (1928), adjusted by Barkman et al. (1964). Percentage coverage was estimated for all vascular plant species in square plots (50 x 50 cm^2) near the sampling points. 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 numbers and species diversity (Shannon-Wiener Diversity Index) (Shannon, 1948) were calculated from these converted data.

Data analysis

We examined the overall responses in riparian plant species richness, diversity, biomass and plant-available N and P to increased drought (decreasing ground water tables), using a set of Linear Mixed Models (LMMs, type I Sum-of-squares). We investigated effects of decreased water tables (water level in cm below soil surface) on the response variables species richness, Shannon diversity, biomass, and plant-available N and P in the soil. In these models mean water table, treatment (drought versus control) and the interaction between mean water table and treatment were incorporated as fixed effects, and study site, year and plot level (elevation along the gradient, i.e. sampling position 1, 2 or 3) as random effects. Treatment was also included as random effect nested within stream. We examined the drought treatment effect by analyzing treatment and the interaction between treatment and mean water table as the main factors in the model. The Linear Mixed Models were all performed within the R statistical environment (R

Core Team, 2018), using LMER (Bates et al., 2015) and LMER_test (Kuznetsova et al., 2015). Confidence intervals for the Linear Mixed Models were performed using bootpredictlme4 (Duursma, 2019). Visualization of statistics were performed by ggplot (Wickham, 2016), sjplot (Lüdecke, 2018c) sjmisc (Lüdecke, 2018b), sjlabelled (Lüdecke, 2018a), visreg (Breheny & Burchett, 2017) and gridextra (Auguie, 2017).

Variation in riparian plant species composition across the range of measured environmental conditions was analysed using a Detrended Correspondence Analysis (function decorana), for all streams considering all years, for 2011 and for 2013 using vegan (Oksanen et al., 2018) in the R statistical environment (R Core Team, 2018). In addition, environmental vectors were fitted to the ordination for mean water table, available N and P using the function envfit (Oksanen et al., 2018).

Results

We performed the drought treatment for an average of 10 weeks, from the end of June to mid-September. At most sites, average water tables decreased at the sampling points of the drought sections compared to control sections, with the strongest decrease occurring at sampling points 2: this decline was on average 12.79 cm (Table 3.1)

Table 3.1. Means and SE of water table depths measured in piezometers at least four times during each experimental run (at the start of the experiment, after 2 weeks, after 4 weeks, and at the end of the experiment). Negative values indicate that the water table was situated below the ground surface. The first sampling point was at the lowest water table of the stream during summer base flow conditions. The second sampling point was just above the normal winter water table that is normally not flooded in either summer or winter (position 2). The third sampling point was at the highest point up the stream valley that could be flooded by surface water during extreme winter floods (position 3).

Site	Treatment	Position	Water table, mean (cm)	Water table, SE
Sandemandsbækken	Control	1	-10.35	1.68
		2	-22.35	1.73
		3	-16.59	1.32
	Drought	1	-18.86	1.44
		2	-26.75	1.89
		3	-20.93	2.45
Voel bæk	Control	1	-10.07	0.94
		2	-16.13	1.01
		3	-29.36	1.56
	Drought	1	-35.23	1.73
		2	-49.35	2.20
		3	-56.10	2.39
Groote Molenbeek	Control	1	-5.27	3.09
		2	-15.87	2.53
		3	-21.52	3.48
	Drought	1	-8.72	1.78
		2	-33.00	2.14
		3	-37.75	3.14
Pego	Control	1	-6.60	4.59
		2	-57.03	4.65
		3	-109.83	4.98
	Drought	1	-7.57	3.70
		2	-77.90	3.59
		3	-121.70	3.68
Caselas	Control	1	-10.10	5.03
		2	-67.40	5.23
		3	-118.57	5.34
	Drought	1	-9.33	6.15
		2	-55.72	4.93
		3	-110.43	5.40

Species richness and diversity

All years and sites combined there was no significant relation between treatment and species richness, but there was a trend towards a steeper decline of species richness with increasing water tables at the drought sections, indicating that at the wetter part of the riparian zone species richness declined more strongly under the drought treatment (Table 3.2, Fig. 3.2). Highest overall species richness was detected at intermediate water tables (0 to 50 cm below soil surface, Fig. 3.2) for all sites and treatments. In the final year of the three-year experiments (2013), this trend was even more clear (interaction effect between water table and treatment, P = 0.054, Table 3.3), indicating that the increased drought episodes had the greatest impact on species richness at the wettest part of the riparian gradient near the streambed. Effects of mean water table, treatment or interaction effect on Shannon diversity were not significant (Table 3.2, 3.3).

Biomass, extractable soil N and P

When considering all experimental years and sites, we found a significantly negative effect of the drought treatment on biomass; biomass was lower in the drought sections compared to the control sections (P = 0.025, Table 3.2, Fig. 3.2). Effects of mean water tables on extractable soil N were also significant: decreasing water tables along the riparian gradient had a strongly significant positive effect on available N (P = 0.009, Table 3.2, Fig. 3.2). Overall, when considering all years and sites, no effects of decreasing water tables on extractable soil P were found (Table 3.2). However, in the last experimental year of the three-year experiments (2013) we found a significant negative effect of decreasing water tables on N (P = 0.001, Table 3.3, Fig. 3.3) and a significant effect of the drought treatment on available P, with a lower availability of P in the drought sections compared to the control sections (P = 0.012, Table 3.3).

Table 3.2. Output from LMM with mean water tables and treatment as fixed effects, their interaction and including year and level as random effects with treatments as random effect nested within streams; all years.

	spec richness			**shannon**			**biomass**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	7.39	5.22–9.57	**<0.001**	1.13	0.92–1.34	**<0.001**	476.20	165.82–786.58	**0.027**
mean groundwater level	-0.00	-0.03–0.02	0.691	-0.00	-0.00–0.00	0.867	-0.47	-2.01–1.08	0.555
drought	-1.43	-3.84–0.98	0.274	-0.17	-0.47–0.13	0.285	-213.63	-318.36–-108.91	**0.025**
mean_groundwater_ level:treatment-drought	-0.03	-0.06–0.00	0.067	-0.00	-0.01–0.00	0.430	-0.92	-2.99–1.15	0.390

Random Effects			
σ2	6.27	0.22	37431.91
τ00	$2.38_{\text{treatment:stream}}$	$0.02_{\text{treatment:stream}}$	$1056.56_{\text{treatment:stream}}$
	2.22_{stream}	0.00_{stream}	$117523.28_{\text{stream}}$
	0.00_{level}	0.00_{level}	312.78_{level}
	0.22_{year}	0.00_{year}	210.94_{year}
Observations	198	198	198
Marginal R^2 / Conditional R^2	NA	NA	NA
AIC	970.935	294.667	2692.009

	available n			**available p**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	16.32	-14.90–47.54	0.341	80.27	-27.40–187.93	0.237
mean groundwater level	-0.39	-0.68–-0.10	**0.009**	-0.17	-0.50–0.16	0.314
drought	-2.25	-19.66–15.17	0.801	11.22	-10.05–32.49	0.303
mean_groundwater_ level:treatment-drought	0.14	-0.23–0.52	0.456	0.33	-0.13–0.79	0.160

Random Effects		
σ2	1287.64	1960.06
τ00	$0.00_{\text{treatment:stream}}$	$0.00_{\text{treatment:stream}}$
	1008.74_{stream}	29.03_{stream}
	40.83_{level}	103.66_{level}
	0.00_{year}	8777.19_{year}
Observations	162	162
Marginal R^2 / Conditional R^2	NA	NA
AIC	1655.753	1725.75

Table 3.3. Output from LMM with mean water table and treatment as fixed effects, their interaction and including year and level as random effects with treatments as random effect nested within streams; 2013.

	spec richness			shannon			biomass		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	9.24	5.78−12.71	**0.001**	1.16	0.79−1.54	**<0.001**	676.57	158.59−1194.54	0.072
mean groundwater level	0.04	-0.03−0.11	0.278	0.01	-0.01−0.02	0.335	-1.43	-6.24−3.38	0.563
drought	-3.44	-8.11−1.22	0.174	0.30	-0.36−0.97	0.379	-208.68	-478.92−61.56	0.151
mean_groundwater_ level:treatment-drought	-0.10	-0.20−-0.00	0.054	0.00	-0.02−0.02	0.895	-0.25	-6.74−6.24	0.940

Random Effects			
σ2	7.38	0.29	32369.45
τ00	2.89 treatment:stream	0.01 treatment:stream	4526.96 treatment:stream
	3.60 stream	0.00 stream	190798.35 stream
	0.00 level	0.00 level	1063.88 level
Observations	54	54	54
Marginal R^2 / Conditional R^2	NA	NA	0.0033 / 0.863
AIC	289.493	103.614	747.469

	available n			available p		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	4.01	1.38−6.65	**0.017**	22.90	11.71−34.09	**0.014**
mean groundwater level	0.09	0.04−0.15	**0.001**	0.14	-0.02−0.30	0.083
drought	0.05	-2.75−2.84	0.975	-13.63	-23.01−-4.25	**0.012**
mean_groundwater_ level:treatment-drought	-0.05	-0.12−0.01	0.119	-0.19	-0.40−0.03	0.097

Random Effects		
σ2	3.28	36.00
τ00	0.54 treatment:stream	7.64 treatment:stream
	2.03 stream	76.15 stream
	1.41 level	0.00 level
Observations	54	54
Marginal R^2 / Conditional R^2	0.166 / 0.623	NA
AIC	248.784	377.099

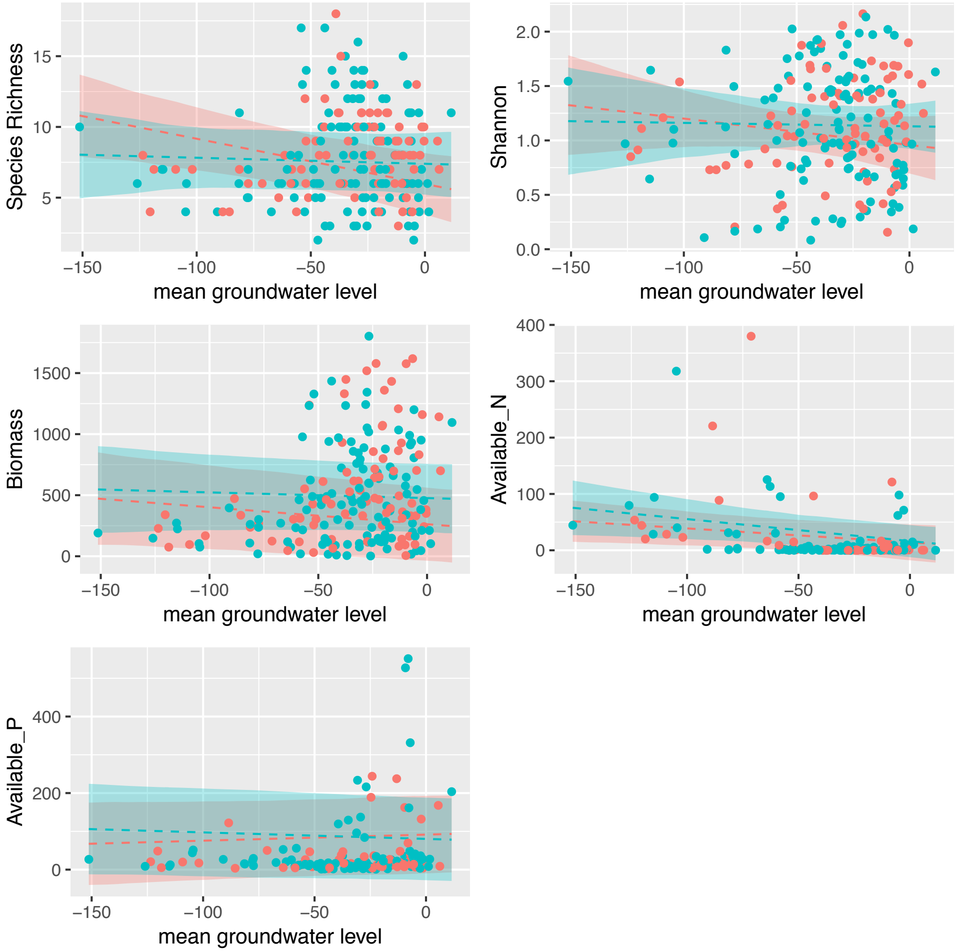


Fig. 3.2. Results of the Linear Mixed Models using year and stream as random effects with treatments nested within the streams for all years. Confidence intervals are calculated with a bootstrap (n=500) via bootpredictlme4 (Duursma, 2019) and visreg (Breheny & Burchett, 2017). Plot includes (1) the expected value (lines), (2) a confidence interval for the expected value (bands), and (3) the original data points. Bands, lines and points are colored according to treatment (blue = control treatment, red = drought treatment).

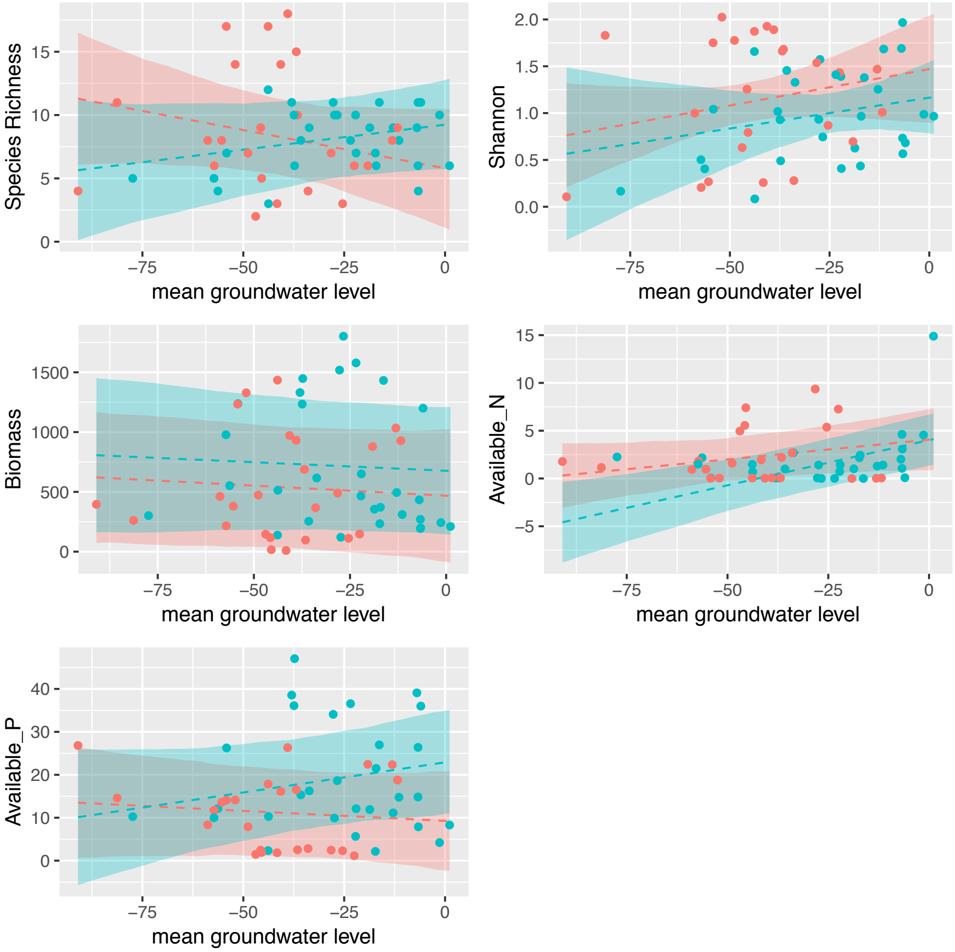


Fig. 3.3. Results of the Linear Mixed Models using stream as random effect and with treatments nested within the streams for 2013. Confidence intervals are calculated with a bootstrap (n=500) via bootpredictlme4 (Duursma, 2019) and visreg (Breheny & Burchett, 2017). Plot includes (1) the expected value (dashed lines), (2) a confidence interval for the expected value (bands) and (3) the original data points. Bands, lines and points are colored according to treatment (blue = control treatment, red = drought treatment).

Riparian plant species composition and environmental variables

A Detrended Correspondence Analysis (DCA) was conducted and riparian plant species composition was plotted for the five European lowland streams for all years together (Fig. 3.4), and for each stream separately (Fig. 3.5). The results demonstrate that streams (and countries) are clearly separated along the first axis: a clear distinction in species composition was found between sites, and especially between different countries. Species composition at the Groote Molenbeek was clearly separated from the Danish and Spanish sites along the axis. For the individual site DCA's, most sites were characterized by a larger ordination area for the drought sections compared to the control sections (Fig. 3.5), showing more variation in species along the riparian gradient in the drought sections.

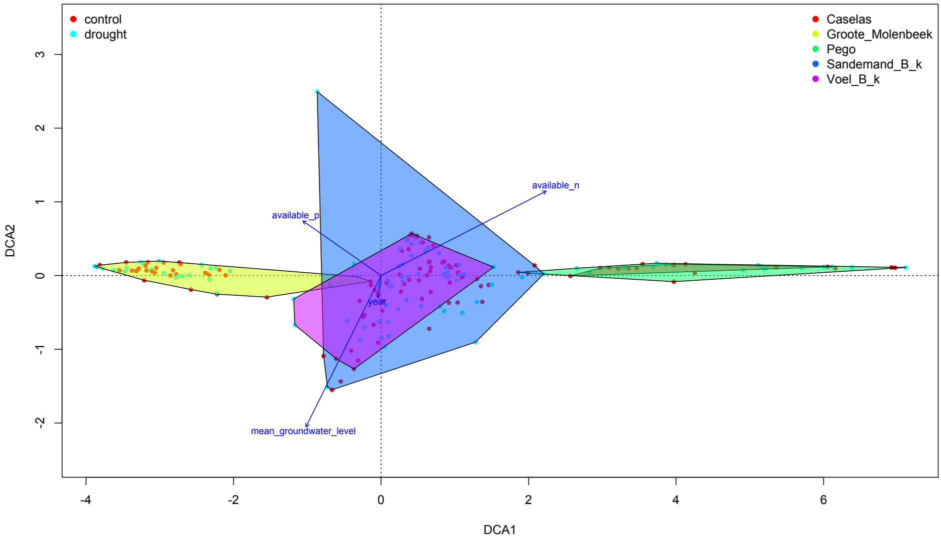


Fig. 3.4. Results of the Detrended Correspondence Analysis, colored by stream including an environmental fit for all years together. Streams (and countries) are clearly separated along the first axis. Points are colored according to treatment (control vs. drought). Abbreviations of environmental fit indicate available nitrogen (n) or phosphorus (p) and mean water table (GWL).

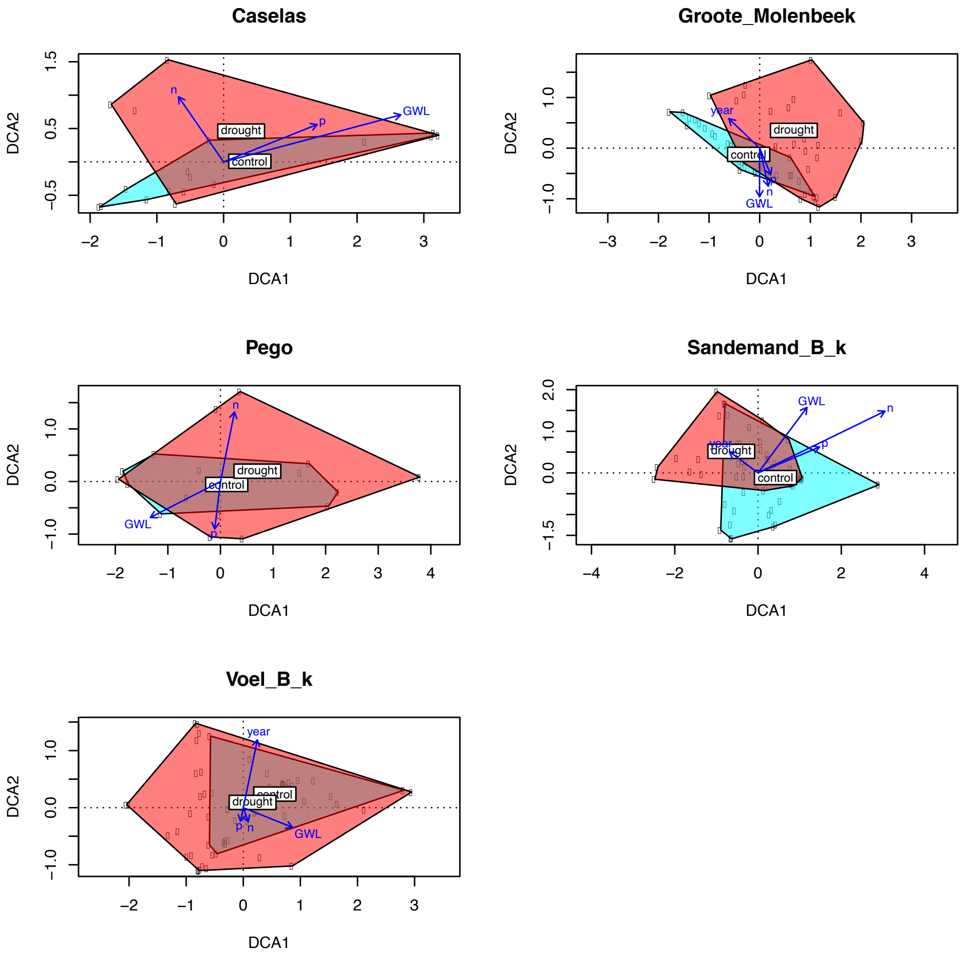


Fig. 3.5. Results of the Detrendend Correspondence Analysis (DCA), with subsequent envfit biplot arrows. Polygons indicate treatments with drought (red) and control (blue). All sites were given equal weights in finding factor averages of environmental variables.

Discussion

The effect of the drought treatment implemented in this study (10 weeks a lowered groundwater table by on average 10.15 cm) was relatively mild at all sites. This relatively small reduction in water tables is estimated to be realistic in representing future drier summers. However, the mild effect of our experiment along this Atlantic climate gradient was also likely due to considerable rainfall during the experimental years, especially in 2011 and 2012. Only in 2013 there were dry conditions during July and August due to lower rainfall than in normal years (S3.1). As a consequence, during the first two years of the experiment there seemed to be little drought stress for the plants due to considerable rainfall, and we observed little or no plant mortality. Still, species richness was found to be slightly affected by the drought treatment. At the end of the third experimental year and over all years, we found a trend towards a decrease in species richness with declining water tables at the lowest locations of the riparian zones near the streambed. We observed no effect on Shannon diversity. This suggests that only prolonged periods of drought with little rainfall and strong evaporation, such as occurred across Europe in 2018 (JRC, 2018), are likely to affect the species richness and diversity of this type of lowland, rain-fed streams.

We did find a significant increase in extractable soil N with declining water tables across all years of our experiment and a decrease in extractable soil P during the last experimental year. This is in line with what we expected; higher temperature and oxygen content in drier soils often leads to higher decomposition and mineralization rates (Mitsch & Gosselink, 2015). This effect apparently already occurs when water tables decrease relatively mildly, and despite sufficient rainfall in between drought spells to maintain plant growth. Also, iron(hydr)oxides formed under aerobic conditions have the ability to capture phosphate which may have resulted in a decrease in extractable soil P. However, the availability of N or P did not show clear relations to plant biomass in our data; when considering all years we only found a general pattern of significantly lower plant biomass at the drought section than at the control. Probably, the drought induced by our experimental treatment did not induce plant mortality, but was sufficient to limit plant growth. This result is in accordance to our previous meta-analysis which confirmed that in riparian plants, biomass reduction precedes mortality under drought conditions (Garssen et al., 2014).

Clearly, the strongest differentiation in vegetation composition between the sites occurred along the climatic gradient. Climatic conditions (rainfall, temperature, length of the growing season) strongly determine species composition, as well as local abiotic conditions, which play an important role as well (Baattrup-Pedersen et al., 2018). Together, these factors are likely to explain the large variation between the countries and sites. Similarity in species composition between the different countries was low, especially when comparing species composition in the Spanish riparian zones with the Dutch and Danish sites. Four similar species were detected in all three countries: *Holcus lanatus, Stellaria media, Rununculus repens* and *Urtica dioica*, all common and ruderal species. These differences in composition overruled any signals of drought, but when comparing drought sections to control section within each site, it became clear that the polygon encompassing the drought treatment plots was generally a bit wider than the polygon of the control plots, suggesting an increased variation in species.

Another paper based on our experiment, but with a focus on structural and functional responses of riparian plant communities, showed that taxonomic diversity initially declined in response to drought (although not significantly so in all years) and later on remained stable under these conditions. This decline in taxonomic diversity in response to drought was only evident near the streambeds (Baattrup-Pedersen et al., 2018). It is expected that extreme drought conditions, that dry out the streambed and diminish the survival of hydric species, will narrow the riparian wetland zone with typical hydric species, particularly at a relatively short distance to the streambed.

In conclusion our research on prolonged drought episodes in the Atlantic region demonstrated that a relatively short period of decline in surface water levels did have a fairly small impact on riparian vegetation. In general, the effects of relatively short drought episodes on the vegetation in or near the streambed are stronger compared to effects on the riparian vegetation higher up the riparian zone, probably because the lower elevation vegetation is more dependent on surface water levels and high soil moisture levels.

For the maintenance of overall species diversity, wide riparian zones with a gradual slope are important. A natural and gradual riparian zone can accommodate more species (Fraaije et al., 2015b), since hydrological niches form the basis for species coexistence along hydrological gradients (Silvertown et al., 1999). Preservation and if needed restoration of this natural riparian habitat heterogeneity is therefore likely to promote species coexistence and biodiversity (Fraaije et al., 2015b). Restoration efforts may enhance species richness and strengthen ecosystem resilience of stream riparian wetlands under a changing climate.

Acknowledgments

The authors thank the water boards, landowners and nature organizations for permission to carry out the experiments. We thank Wageningen Environmental Research for the nice collaboration within the REFRESH project to carry out the drought experiment in the Netherlands. This work was supported by the European Union 7th Framework Project REFRESH under contract no. 244121. Special thanks to Edwin Pos (Utrecht University) for statistical analyses and several students for their assistance during experimental work.

Supporting information

S3.1. Average precipitation displayed per month in L/m^2 for each study site and deviation from normal precipitation (1981-2010 period for the Netherlands, 2006-2015 period for Denmark and 1982-2012 period for Spain).

Period	Sandemands-baekken and Voel baek (Denmark)	Deviation from normal prec.	Groote Molenbeek (the Netherlands)	Deviation from normal prec.	Caselas and Pego (Spain)	Deviation from normal prec.
July 2011	80	-8	88	+15		
August 2011	125	+25	132	+54		
September 2011	110	+35	33	-26		
July 2012	100	+38	109	+36	14	-43
August 2012	87	+16	43	-36	65	-1
September 2012	125	+50	51	-8	74	-12
July 2013	25	-47	46	-27		
August 2013	60	-40	29	-49		
September 2013	77	-33	130	+70		

Chapter 4

Riparian plant community responses to increased flooding: a meta-analysis

Annemarie G. Garssen, Annette Baattrup-Pedersen, Laurentius A.C.J. Voesenek, Jos T.A. Verhoeven and Merel B. Soons

Global Change Biology (2015), 21, 2881–2890
doi: 10.1111/gcb.12921

Abstract

A future higher risk of severe flooding of streams and rivers has been projected to change riparian plant community composition and species richness, but the extent and direction of the expected change remain uncertain. We conducted a meta-analysis to synthesize globally available experimental evidence and assess the effects of increased flooding on (1) riparian adult plant and seedling survival, (2) riparian plant biomass and (3) riparian plant species composition and richness. We evaluated which plant traits are of key importance for the response of riparian plant species to flooding. We identified and analysed 53 papers from ISI Web of Knowledge which presented quantitative experimental results on flooding treatments and corresponding control situations. Our meta-analysis demonstrated how longer duration of flooding, greater depth of flooding and, particularly, their combination reduce seedling survival of most riparian species. Plant height above water level, ability to elongate shoots and plasticity in root porosity were decisive for adult plant survival and growth during longer periods of flooding. Both 'quiescence' and 'escape' proved to be successful strategies promoting riparian plant survival, which was reflected in the wide variation in survival (full range between 0 and 100%) under fully submerged conditions, while plants that protrude above the water level (>20 cm) almost all survive. Our survey confirmed that the projected increase in the duration and depth of flooding periods is sufficient to result in species shifts. These shifts may lead to increased or decreased riparian species richness depending on the nutrient, climatic and hydrological status of the catchment. Species richness was generally reduced at flooded sites in nutrient-rich catchments and sites that previously experienced relatively stable hydrographs (e.g. rain-fed lowland streams). Species richness usually increased at sites in desert and semi-arid climate regions (e.g. intermittent streams).

Introduction

Climate change is projected to increase the magnitude and frequency of intense precipitation events in the near future (Intergovernmental Panel on Climate Change (IPCC), 2007; Bates et al., 2008), thus sharpening the contrasts between wet and dry regions and wet and dry seasons (Intergovernmental Panel on Climate Change (IPCC), 2013). These changes will have significant effects on the hydrological interaction between rivers or streams and their riparian zones, with implications for the ecology of both types of ecosystems. In most temperate regions, such as northern and Central Europe, annual precipitation is expected to increase, particularly in the cold season, but also in the growing season, although there is a much wider spread of projected changes in the latter period (Frei et al., 2006; Christensen & Christensen, 2007; Dankers & Feyen, 2009; Feyen & Dankers, 2009; Intergovernmental Panel on Climate

Change (IPCC), 2013). This will result in a consistently higher flood risk from streams and rivers (Dankers & Feyen, 2009; Hirabayashi et al., 2013) and can be assumed to have major impacts on their riparian zones, affecting soil processes and vegetation dynamics (Naiman & Decamps, 1997; Poff et al., 1997; Merritt et al., 2010).

The riparian zone extends from the stream across the floodplain, including the whole area that is influenced by the waterway (Gregory et al., 1991; Naiman & Decamps, 1997; Naiman et al., 2005). Riparian ecosystems are diverse, dynamic and complex habitats (Naiman et al., 1993; Naiman & Decamps, 1997); they are highly sensitive to changes in catchment land use and are among the most degraded and impacted ecosystems in the world (Tockner & Stanford, 2002). The magnitude of discharge and the depth, frequency, duration and timing of floods all affect riparian zones (Poff et al., 1997). As riparian ecosystems are (at least partly) rain-fed systems, which are also influenced by overland and shallow subsurface flows as well as deeper groundwater pathways, they are sensitive to precipitation changes (Poff et al., 1997; Garssen et al., 2014). Gradients in wetness and fluvial disturbance strongly govern riparian vegetation composition, structure and abundance (Auble et al., 1994; Voesenek et al., 2004; Merritt et al., 2010; Fraaije et al., 2015a). Communities are organized across the riparian zone according to differences in the specific environmental niches of the constituent species, often resulting in distinct vegetation belts along the gradient from wet to dry (Silvertown et al., 1999; Ström et al., 2011), which find their origin already in early plant recruitment phases (Fraaije et al., 2015a). The lower distribution limits are normally constrained by flooding stress, while drought is more important at the upper distribution limits (Silvertown et al., 1999; Lenssen & de Kroon, 2005; Garssen et al., 2014; Fraaije et al., 2015a).

As such, an increase in flooding frequency can be expected to affect species distribution limits and communities through a series of physical and ecological changes across the riparian zone. Direct effects of flooding may include the following: (1) mortality of established plants and the suppression of dominant species, thereby facilitating species coexistence and/or the establishment of species better adapted to new hydrological regimes (Naiman & Decamps, 1997; Osterkamp & Hupp, 2010; Ström et al., 2012); (2) mobilization, transport and deposition of seeds (Jansson et al., 2000, 2005; Goodson et al., 2003), thereby facilitating new establishments and species turnover; (3) an increase in nutrient-rich sediment deposits (Craft & Casey, 2000; Kronvang et al., 2009; Noe et al., 2013), leading to a shift towards more productive species, which especially in intensively used catchments may result in a loss of riparian species (Baattrup-Pedersen et al., 2013a); and (4) temporal and more long-term changes in the environmental conditions in the riparian zone, which are critical for plant growth and survival, particularly oxygen and nutrient availability, addressed below.

The mechanisms and plasticity of plant species to tolerate flooding vary greatly, being largely species-specific and reflective of the species arrangement along the riparian elevational gradient (Visser et al., 2000; Chen et al., 2002; Voesenek et al., 2004; Lenssen & de Kroon, 2005). The depth, frequency, duration and timing of flooding are all decisive for the survival of plant species (van Eck et al., 2004, 2005; Voesenek et al., 2004). Plants are considered to be most sensitive during the growing season: van Eck et al. (2006) demonstrated that species survived winter floods for a longer period compared to summer floods. While many wetland plants can tolerate a saturated soil, a situation in which plants are partly or fully submerged is more critical for their survival. A saturated soil causes oxygen deficiency for the roots, while complete submergence disrupts the connection with the atmosphere, limiting gas exchange further and thus also photosynthesis. Plant strategies to tolerate flooding include many physiological adaptations to withstand oxygen and carbon dioxide shortage and mechanical stress. The 'escape strategy' permits the plant to regain contact with the atmosphere to improve availability of light, carbon dioxide and oxygen (Laan & Blom, 1990; Bailey-Serres & Voesenek, 2008). This strategy may include shoot elongation (Voesenek et al., 2004), aerenchyma formation (increased root porosity) to improve internal oxygen transport (Laan et al., 1990; Visser et al., 2000), adventitious root formation (Chen et al., 2002), underwater photosynthesis (Banach et al., 2009), gas films around leaves (Pedersen et al., 2009), anatomical leaf changes (Insausti et al., 2001) and development of a barrier to radial oxygen loss (Jackson & Armstrong, 1999). On the other hand, the 'quiescence strategy' allows the plant to survive as long as possible under unfavourable conditions, most prominently low oxygen levels. This strategy may include low growth rates, the avoidance of high metabolic activity (Geigenberger, 2003) and protection against chemical radial oxygen species (chemically reactive molecules containing oxygen) (Bailey-Serres & Voesenek, 2008). During flooding, stored carbohydrates may prolong survival (Laan & Blom, 1990). When plant species are sufficiently adapted to survive flooding, biomass can be sustained or regrowth can take place after withdrawal of the floodwater. However, if species lack these adaptations, a strong reduction of biomass takes place during flooding (van Eck et al., 2004). Frequently reported responses of riparian plants to waterlogging include wilting and stomatal closure (e.g. Chen et al., 2002), a reduction in net photosynthesis (e.g. Pezeshki, 1993) and, eventually, plant death. Finally, flooding can also have a direct effect on plant growth by reducing light availability (Setter et al., 1997), which may contribute to shape the zonation of riparian plants in river floodplains (Vervuren et al., 2003). More indirectly, flooding events influence riparian biogeochemical cycles that control plant nutrient availability (Olde Venterink et al., 2006).

Given the multitude and complexity of ecological, physiological and biogeochemical responses to increased flooding in the riparian zone, it is difficult to predict flooding effects on riparian plant communities. Yet, given projected climatic changes, such information is crucial for future management plans dealing with the vegetation and biodiversity of these highly vulnerable ecosystems. It is therefore our aim to summarize existing quantitative information on flooding effects on riparian plant communities across the globe. For this purpose, we use a systematic literature review and meta-analysis to evaluate specifically (1) the relation between increased flooding and seedling and adult plant survival, (2) the relation between increased flooding and plant biomass (as indicator of survival and competitive ability on longer timescales), (3) which plant functional traits are most crucial for response success during flooding and (4) responses in riparian plant species richness to increased flooding. Our definition of flooding encompasses both saturated soil conditions (waterlogging) and situations in which plants are partly, or fully, submerged. Effects of increased drought, which are relevant to streams and riparian zones as well, have been addressed in an earlier paper (Garssen et al., 2014).

Materials and methods

For our systematic review and meta-analysis, we searched ISI Web of Knowledge (7th June 2013) for scientific peer-reviewed studies on the effects of (increased) flooding on riparian wetland plant survival, above- and belowground biomass and species richness. We selected specific keyword strings for our search to extract relevant publications (Table S4.1) and supplemented these with relevant cases from publications selected in an earlier analysis on the effects of drought on riparian plants (Garssen et al., 2014). All titles and abstracts were checked for relevance using strict study eligibility criteria: we only selected data from field studies carried out in riparian wetlands along streams or rivers or mesocosm/greenhouse/climate chamber/laboratory experiments with typical riparian wetland plants. Studies from tidal systems, estuaries and lakes were excluded. All selected studies had a before–after (BA), control–impact (CI) or a before–after–control–impact (BACI) design to be able to quantify the effects of flooding. We did not use results from studies on sites with a history of strong disturbance, such as the application of local fertilization, ditch cleaning or mowing. Studies conducted in the temperate Atlantic, continental, boreal, subtropical and (semi)-arid biogeographical regions (worldwide) were included. The systematic literature review also included two studies conducted in the desert region. The meta-analysis concerned studies carried out during periods of active plant growth, while the systematic literature review focused on studies conducted during and after winter and spring flooding.

From the selected studies, we extracted cases linking a single response variable to a single flooding treatment. For the response variables seedling and adult plant survival and plant total biomass (aboveground and belowground), we summarized all available quantitative data in coding sheets. Extra information was included concerning the study system, plant community, the relevant plant traits root porosity (%) and ability to elongate shoots (0 or 1). In case data were not presented in tables, PLOT DIGITIZER 2.6.1 software was used to extract data from graphs. We analysed the responses of plant survival and biomass to flooding by calculating response ratios: the ratio of the treatment (impact) to the control group. Response ratios provide a relative quantification of effect sizes, which is suitable for comparisons between studies (Borenstein et al., 2005). A response ratio >1 indicates a positive change (increased survival or biomass), while a value <1 equals a negative change (decreased survival or biomass). A value equal to 1 means no change. Our literature search on flooding effects on plant species richness did not yield sufficient cases for quantitative analysis using response variables, and this subject was therefore addressed separately (see below).

We investigated effects of increased flooding depth (water level relative to the soil surface, in cm) and duration (days of flooding) on the response variables using regression analysis in SPSS (IBM SPSS Statistics version 20). For reasons of parsimony, we fitted weighted linear regression curves to the response data and replaced these by logarithmic regression curves in only a few cases when linear regressions were not significant. Note that in all figures, results of weighted regression analyses are shown. Weights were assigned by the number of times a case was represented in the data set; for instance, a species' biomass or survival measured once received a higher weight compared to cases measured multiple instances over time (e.g. when a certain experiment involved five measurements of a plant's response over time, a weight of 0.2 was assigned to each case in SPSS). As we considered flooding of the aboveground plant parts as most critical, we used relative plant height to the water level (plant height minus treatment water level, in cm) as a separate factor in our analysis of adult plant survival and biomass. We used general linear mixed models (GLMM) in SPSS with Type II sum-of-squares to assess effects of the covariates flooding depth/relative plant height, duration of flooding and the interaction between these variables on the response ratio of seedling and adult survival, and biomass (IBM SPSS Statistics version 20). These specific analyses could only be applied to a subset of the data, across which both depth and duration varied sufficiently to be able to detect effects. T-tests were conducted to assess overall effects of duration and depth of flooding on survival and biomass. Furthermore, we evaluated the plant traits that were identified in the selected publications as affecting the response success of the respective species during flooding, in plant survival and biomass analyses.

A systematic literature survey was made of 23 studies considering the response of riparian plant species richness and species composition to an increase in duration, depth and frequency of flooding. We evaluated cases in which flooding positively or negatively affected these vegetation characteristics. Here, we did include results on the impact of restoration as long as the upper soil layer had not been totally removed. We extracted relevant details of the main effects on species richness, observations, responsible mechanisms, biogeographical region and research set-up. We summarized these details in a descriptive table (Table S4.7).

Results

In total, 1205 publications emerged from our search query in Web of Science (Table S4.1). A selection based on our eligibility criteria resulted in 53 unique publications that met the strict criteria for our analysis, from which 8 were used in both biomass and survival analyses. In total, 18 studies contained quantitative data on the effects of flooding on seedling and adult plant survival (Table S4.2), 21 reported on the effects of flooding on plant total biomass (Table S4.3), and 22 reported on the effects of flooding on species richness and/or species composition (Table S4.6). An overview of all species included in our meta-analysis, and available data on the relevant characteristics and traits of these species, is given in Table S4.5.

Survival

The studies on the impact of flooding on seedling survival differed in flooding depth from 0 cm (soil saturated conditions) to 100 cm (water level above soil level) and in flooding duration from 10 to 214 days. They had corresponding control situations with drained, unsaturated or 'normal' conditions. The studies were conducted in the semi-arid (3 studies), Atlantic temperate (3), continental temperate (2) and subtropical (1) regions. The adult plant survival studies covered flooding depths ranging from 0 cm to 100 cm and flooding duration from 3 to 90 days. The majority of these studies were conducted in the Atlantic temperate region (7 of 9 studies).

Despite a wide variation in responses between treatments and species, regression analyses show a significant negative effect of flooding on seedling and adult plant survival (note that regression lines represent the result of weighted regressions). A longer duration of flooding strongly reduces both seedling (Fig. 4.1a; t-test: $P < 0.0001$) and adult plant survival (Fig. 4.1b; t-test: $P < 0.0001$); for reasons of parsimony, it can be assumed that survival is reduced more or less linearly with increased duration of flooding across all investigated species (Table 4.1). Although from the graph it may appear that seedlings are less sensitive to flooding, this can be caused by the lack of data for adult plants in the range of 100–220 days. The relation between flooding depth and the response ratio of seedling survival does not suggest any effect of depth on seedling survival, but rather that a wide variation exists among species and experimental settings (Fig. 4.2a). When considering flooding depth relative to plant height (which was possible only for adult plants as seedling height was not given in most studies) (Fig. 4.2b), the relation becomes more complex. While a significant positive linear relationship exists between increasing height of the plants above the water level and the probability of survival, there is also statistical support for a nonlinear relation (logarithmic regression, Table 4.1). In any case, there is much variation in survival (full range between 0 and 100%) under fully submerged conditions, whereas plants that protrude above the water level (>20 cm) almost all survive.

Although only few data were available, we find evidence that the relations between survival and flooding duration are affected by the ability of the plant species to elongate shoots (N = 11 species, 66 cases for seedling survival, Fig. 4.1c; N = 10 species, 42 cases for adult plant survival, Fig. 4.1d; Table 4.1). Plant species able to elongate their shoots show no significant relation between survival response and flooding duration, whereas plant species unable to plastically elongate their shoots show declining survival over time (Fig. 4.1c,d). Insufficient data were available to meaningfully test for relations between shoot elongation ability and response to increasing flooding depth. GLMM analyses (see Methods) suggest that there is an interaction between effects of flooding depth and duration on seedling survival, with survival being reduced most when deep and long flooding treatments are applied (Table 4.2).

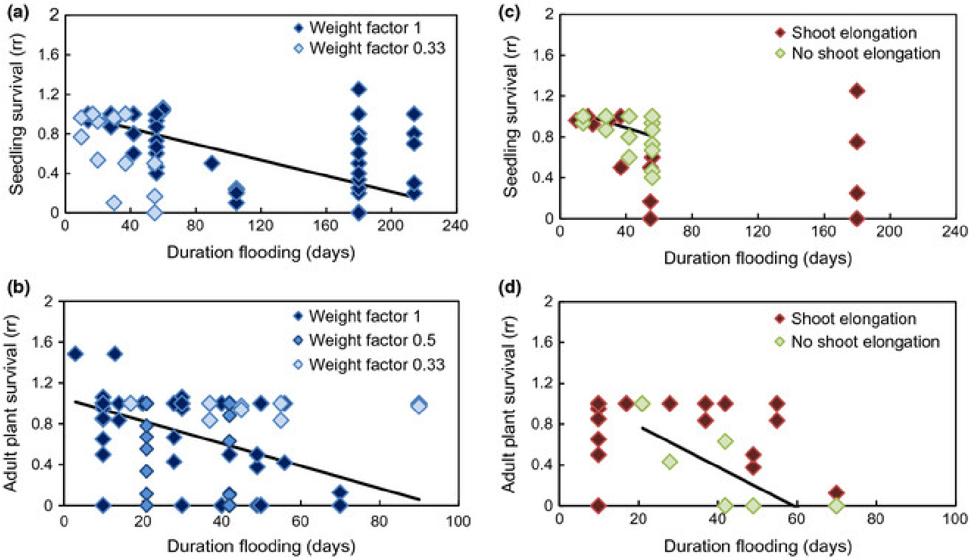


Fig. 4.1. Effects of duration of flooding on the response ratio of seedling survival (a, c) and adult plant survival (b, d) for different riparian species (mean number of seedlings or adult plants in treatment/ seedlings or adult plants in control). Weighted regression analyses are shown. Weight factors were assigned to correct for the number of times a case was represented in the data set. Panels a and b show all data points; panels c and d present only data points for which presence or absence of shoot elongation is known. Panel a: n = 123 cases, total number of species = 34, from nine studies. Panel b: n = 113, species = 33, nine studies. Panel c: n = 66, species = 11, four studies. Panel d: n = 42, species = 10, four studies.

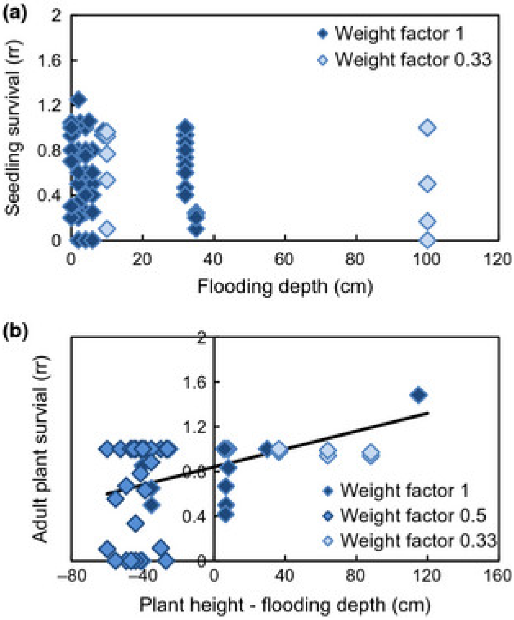


Fig. 4.2. Response ratio of survival (mean number of seedlings or adult plants in treatment/seedlings or adult plants in control) in relation to flooding depth (for seedlings) or in relation to relative plant height (plant height minus flooding depth) for adult plants. Weighted regression analyses are shown (as in Fig. 1). Panel a: n = 123 cases, total number of species = 34, from nine studies. Panel b: n = 113, species = 33, nine studies.

Table 4.1. Equations, R^2 and P-values of regression lines of data points in the respective figures

Figure	Equation	R^2 value	P value
4.1a	y = 0.004x + 1.016	0.433	<0.0001
4.1b	y = 0.011x + 1.047	0.203	<0.0001
4.1c	y = 0.005x + 1.090	0.251	0.001
4.1d	y = 0.020x + 1.182	0.646	0.054
4.2a	y = 0.007x + 0.514	0.126	<0.0001
4.2b	y = 0.004x + 0.840	0.232	0.002
	y = 0.523 + 0.079 ln (x)	0.102	0.05 (not shown)
4.3a	y = 0.001x + 0.538	0.014	0.189
4.3b	y = 0.021 + 0.149 ln (x)	0.122	0.003
4.3c	y = 0.018x + 0.762	0.249	<0.0001
4.3d	y = 1.148 + 0.488 ln (x)	0.461	0.031

Biomass

Experimental conditions in the studies that tested the effect of flooding on total adult plant biomass showed a range in flooding depth from 0 to 100 cm and a duration of 3 to 214 days. Control treatments had a well-drained top soil. The majority of studies looking into effects of flooding on biomass were carried out in the continental region (14 of 21 studies). Interestingly, and in contrast to results found on survival, flooding duration had no significant effect on the amount of total biomass (R^2 = 0.014, P = 0.189, Fig. 3a). Moreover, at increasing flooding duration, riparian plants appeared to have adjusted their root porosity more strongly (Fig. 4.3c).

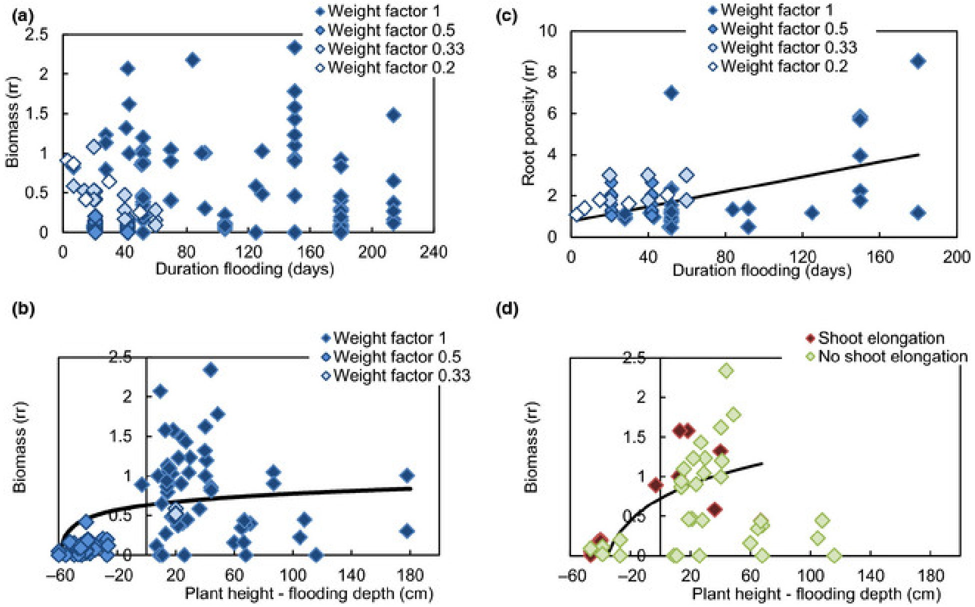


Fig. 4.3. Riparian adult plant biomass response ratio (mean biomass in flooding treatment/mean biomass in control) in relation to duration (a) and relative plant height (plant height minus flooding depth) (b, d). Response ratio of root porosity (mean root porosity in flooding treatment/mean root porosity in control) in relation to duration of flooding (c). Weighted regression analyses are shown. Panel a: n = 154 cases, total number of species = 76, from 21 studies. Panel b: n = 154, species = 76, 21 studies. Panel c: n = 74 cases, species = 35, 13 studies. Panel d: n = 60, species = 33, eight studies.

Across the wide range of treatments (37) and species (76) involved, a largely negative effect of increased flooding depth on total biomass of riparian wetland plants was observed (t-test: $P < 0.0001$, response ratio <1). Regression analysis revealed that the proportion of the plant protruding the water level was a critical factor: in all cases, fully inundated plants suffered severe biomass loss (even though they may survive, Fig. 4.2b), while plants with leaf parts in the air showed a wide range of responses, from severe losses to even enhanced growth (Fig. 4.3b). Particularly for plant species able to elongate shoots, there is a significant positive relation between relative plant height and the response ratio of biomass (for plants unable to elongate shoots, this relation was N.S.; Fig. 4.3d). We could not identify any relation between biomass response across different flooding depths and plant root porosity (P = 0.561). Again, GLMM analyses on part of the total data set suggest that there is an interaction between effects of relative plant height and duration on biomass, with biomass being reduced most when relatively deep and long flooding treatments are applied (Table 4.2).

Table 4.2. Results of three GLMMs for the dependent variables 'response ratio seedling survival' (a), 'response ratio adult plant survival' (b), and 'response ratio biomass' (c). The independent variables include flooding depth (relative plant height for adult plant survival and biomass; all in cm), duration (in days) and interaction effects.

(a) Coefficients	B value	*P* value
Depth	–0.009	0.065
Duration	–0.003	0.002
Depth*duration	0.000	0.000
(b) Coefficients		
Relative plant height	0.003	0.034
Duration Relative plant	–0.007	0.010
height*duration	4.562E-005	0.333
(c) Coefficients		
Relative plant height	–0.014	0.008
Duration Relative plant	–0.004	0.055
height*duration	0.000	0.027

Plant traits and adaptations to flooding events

In the studies selected for our survival and biomass analyses, many different morphological adjustments to the plants' roots, shoots and leaves might have played a role in the actual responses of riparian plants to increased flooding. In Table S4.4, we summarize which plant traits have been identified as affecting the plant species response to flooding in the selected studies and the number of publications in which the trait was explanatory for the response success. Shoot elongation and increased root porosity were mentioned most frequently: in 9, and 8 of 39 papers, respectively, these traits were identified as decisive plant traits to cope with flooding stress.

The majority of studied species were herbs (43 of 94 studied species) and helophytes (21 species), while tree species were studied less frequently (only 11 species) (Table S4.5).

Riparian plant species richness and species composition

The set of publications with data on the effects of increased flooding on riparian plant species richness or species composition contained nine publications reporting a decrease in species richness, seven reporting an increase and two reporting no significant effect (Table S4.7). Four publications provided results on the effects of flooding on species composition and not on species richness. The selected publications differed in research set-up and involved different types of streams and rivers, but they all assessed the effects of increased winter or spring flooding on riparian plant communities.

A variety of responses and mechanisms related to increased winter or spring flooding were reported, leading to an increase or decrease in species richness and changes in species composition. The majority of studies reporting negative effects of flooding on species richness were conducted in the more northern located Atlantic and boreal region (7 of 9 studies), while most studies reporting positive effects were conducted in the semi-arid or desert region (4 of 7 studies) where water scarcity plays a role. The negative effects of flooding on species richness were often related to a relatively high nutrient input from the flood water, leading to eutrophication and an increase in the abundance of productive species (4 of 9 studies; Wassen et al., 2003; Beltman et al., 2007; Baattrup-Pedersen et al., 2013a,b). Also, extreme flood events at sites with a normally stable yearly discharge may lead to a reduction in species richness (6 of 9 studies; Petit et al., 2001; Beltman et al., 2007; Renöfalt et al., 2007; Ström et al., 2011; Baattrup-Pedersen et al., 2013a,b).

Unfortunately, the identity of the species lost or gained was often not mentioned. Hence, little information is available on the effects on rare or typical riparian wetland species. However, in some studies, information was provided regarding the type of species affected by flooding, such as a shift towards more productive species (Baattrup-Pedersen et al., 2013a), the promotion of tall forbs and later on, graminoids (Beltman et al., 2007), and an increase in pioneer species (Stromberg et al., 2007, 2009).

Discussion

As a result of the types of data that were available in the literature, our meta-data analysis was separated into: (1) analysis of the responses of the survival and growth of individual plant species to flooding stress under controlled conditions in laboratory, greenhouse or garden experiments and (2) studies investigating effects of flooding on entire plant communities (reporting on species richness and/or species composition) in the field. For our meta-analysis, we found no studies (meeting our criteria) quantifying individual species responses to natural flooding in the field and no studies reporting on plant community changes under controlled conditions. Thus, a first recommendation arising from our work is to call for more research approaches combining both research lines in future studies.

Experimental data under controlled conditions show that, not surprisingly, longer duration of flooding leads to a reduction of seedling and adult riparian plant survival. More detailed analyses considering possible underlying mechanisms point out that, across the studies here examined, this reduction in survival exists predominantly in species that do not have the plasticity to elongate their shoots under water.

Interestingly, longer duration of flooding per se did not result in lower riparian plant biomass. This is perhaps explained by the fact that the species that survive show a wide variation in biomass responses across the full range of flooding durations. Another possible mechanism here may be that at increasing flooding duration plants may have adjusted their root porosity more strongly as a means to survive prolonged flooding. Our analyses confirm that an increase in flooding depth negatively affects plant survival and biomass (dry weight) and unequivocally demonstrate that it is critical to what extent the plant protrudes above the water level. Even when protruding, the proportion of the aboveground plant that is emerged positively relates to the response of plant survival and biomass. Again, survival and biomass production appear to be critically influenced by the presence or absence of adaptations to withstand flooding conditions, with especially species able to elongate their shoot above the water table being able to survive or even increase biomass, indicated as the escape strategy (Voesenek et al., 2004). Another strategy to survive flooding is quiescence, and when combining our results considering the responses of adult plant survival and biomass, we can conclude that quite a number of plant species are able to survive flooding, but with a very much reduced biomass compared to the control. In summary, our analyses on biomass and survival show that most plants that are under water either do not survive or drastically reduce their biomass, while plants that remain in contact with the atmosphere, either due to the flooding treatment (plant not submerged) or due to shoot elongation, survive, elongate further and gain biomass. Hence, our analyses indicate that both the escape strategy and the quiescence strategy are functional in promoting for the survival of riparian plants during flooding.

Apart from plasticity in shoot elongation, formation of aerenchyma (plasticity in root porosity) is an important trait determining the plant's biomass response to flooding. The formation of both adventitious root systems and aerenchyma in the root cortex are plastic responses of species to meet oxygen demands during flooding (Justin & Armstrong, 1987; Laan & Blom, 1990; Laan et al., 1990; Pezeshki, 1991; Colmer et al., 1998; Visser et al., 2000; Catford & Jansson, 2014). Another morphological adjustment that might be important in relation to biomass change and survival during flooding is stomatal closure and reduced stomatal conductance, which we did not, however, include in our meta-analysis due to lack of data. Stomatal closure and reduced conductance allow the plant to avoid water deficits during flooding (Smith

& Moss, 1998; Nakai et al., 2010) but may limit net photosynthesis due to diffusional limitations on gas exchange (Pezeshki, 1993). A reduction in stomatal conductance is often accompanied by a reduction of biomass and increased mortality (Smith & Moss, 1998), and as such, this may be one of the main mechanisms underlying the quiescence strategy. As shown in Table S4, shoot elongation and increased root porosity were most frequently identified as decisive plant traits to cope with flooding stress. However, as not all studies report on all possible response mechanisms, these statistics may rather suggest that shoot elongation and increased root porosity play at least a role in many cases, whereas other mechanisms may be deemed less relevant by the respective investigators.

From the above, it can be concluded that the responses of riparian plant species to increased flooding depth and duration are complex and species-specific and that it greatly depends on flooding depth, which is reflected in different responses between plants growing in waterlogged soils compared to plants that are fully submerged. The great majority of species used in our analysis on biomass are emergent, which means that their stems and leaves are adapted to protruding above the water. Our results show that many of these species produce more biomass in the flooded situation compared to the control. In these cases, the flooding treatment was fairly mild; only the roots were under water (water level at soil surface) or the depth of flooding did not exceed the plant's height. The lack of biomass increase during flooding in other species, for example *Rumex acetosa,* can be caused by the poor capacity of the species for internal gas diffusion related to low shoot and root porosities (Pierik et al., 2009).

As all experiments included in the meta-analysis have been carried out (at least partly) during the period of active growth of the plants, the magnitude of the reported plant responses is especially relevant for increased flooding during the growing season. The vegetation responses documented in the literature review were all measured under field conditions, with flooding events in winter and early spring. Field studies reporting on effects of increased flooding mention negative and positive responses of species richness, depending on site characteristics (nutrient status, climatic conditions and flow variability). Only in a few papers, changes in the occurrence of characteristic or rare species are mentioned. As these studies focus on different types of riparian plant communities, it is not possible to generalize from them. The reduction in species richness due to flooding might be caused by strong anoxic conditions, which leads to a stressful environment and, eventually, plant death (Renöfalt et al., 2007), followed by replacement by more common species (again, particularly in intensified catchments). In contrast, relatively mild flooding events at sites with more frequent water level fluctuations during the year may have positive effects on species richness (Hughes & Cass, 1997; Capon, 2005; Jansson et al., 2005; Stromberg et al., 2007, 2009). A better oxygenation of the root zone, through high groundwater turnover, might explain the reduction of negative effects of flooding (Renöfalt et al., 2007). These findings are in line with the intermediate disturbance theory (Pollock et al., 1998), which states that intermediate disturbance leads to species-rich communities, while a too high disturbance results in species losses. Other mechanisms positively affecting riparian plant species richness include the establishment of typical pioneer species, of which several are connected to endangered habitats, or flood dependent species stimulated by flood events (Stromberg et al., 2007, 2009), an increase in seed dispersal and seed deposition (Hughes & Cass, 1997; Jansson et al., 2005) and an increase in spatial heterogeneity (Baattrup-Pedersen et al., 2005; Capon, 2005). It is important to realize that riparian wetlands serve as corridors for dispersal (Soons, 2006; Verhoeven et al., 2008). As colonization is limited by dispersal (Brederveld et al., 2011), the substitution of riparian wetland species by species better adapted to new flooding regimes is likely facilitated by source populations in the upstream riparian zone.

All combined, a substantial increase in flooding duration and amplitude (depth) can safely be assumed to strongly affect riparian plant communities in the near future. Plant communities are expected to change towards communities with a relatively high number of flood-tolerant species, caused by mortality of species that are not sufficiently adapted, and in catchments with high-nutrient loadings from stream water and sediment, also towards communities reflective of high-nutrient availabilities. Our literature review indeed shows examples that an increase in duration, intensity and frequency of flooding can lead to a shift in species composition towards more hydric species. A projective study in the boreal zone predicts that a mean annual increase in flood duration may lead to an increase in size of the amphibious vegetation belt near the stream, while the commonly more species-rich graminoid belt, as well as the willow shrub, and riparian forest belt are expected to narrow, leading to a decrease in overall riparian species richness (Ström et al., 2012).

Based on our literature survey, we suggest that increased flooding is likely to result in initial species losses in riparian zones characterized by previously relatively stable hydrographs, but that low-nutrient catchments with source populations (in nature areas, e.g.) upstream may shift towards new, more dynamic species-rich systems. In riparian zones where the frequency and depth of new flooding regimes are too high, however, and in catchments with high-nutrient loadings, increased flooding is much more likely to result in continued species losses. This is particularly relevant as climate models predict the most profound increase in flood frequency to take place in western Europe (Dankers & Feyen, 2009; Rojas et al., 2012; Hirabayashi et al., 2013) where nutrient loading is generally high, the availability of seed sources upstream generally limited and negative effects on species richness of riparian zones pose a realistic threat to their already problematic conservation status. These changes in vegetation composition can occur relatively fast. In a reciprocal transplant experiment in Sweden, for example, where changes in flooding were simulated, a complete transition in species composition was predicted to take place within a decade (Ström et al., 2011). Yet, the speed of change will in reality be connected to the magnitude of the change in flooding regime, which remains difficult to predict (Dankers & Feyen, 2009; Intergovernmental Panel on Climate Change (IPCC), 2013). This stresses the importance of linking regional and spatial information on riparian vegetation and stream flow characteristics for reliable effect predictions (Merritt et al., 2010), the conservation of streams and their riparian zones at the landscape or catchment scale (Verhoeven et al., 2008; Brederveld et al., 2011) and the inclusion of riparian zones in international water legislation such as the Water Framework Directive.

Acknowledgements

This work was supported by the European Union 7th Framework Project REFRESH under contract no. 244121. The authors wish to thank Saskia Burgers (Wageningen University and Research Centre) and Rob Fraaije (Utrecht University) for statistical advice and Anne Mette Poulsen (Aarhus University) for editorial support.

Supporting information

Table S4.1. Keyword strings and results.

Subq. 1: Flooding effects on biomass production
"flooding" AND "biomass*" AND ("plant*" OR "vegetation") → 591 results → refined with "ripar*" OR "stream*" OR "river*" OR "floodpl*" OR "restor*"→ 223 results

Subq. 2: Flooding effects on survival
"flooding" AND "seed*" AND ("plant*" OR "vegetation") → 1036 results → refined with "ripar*" OR "stream*" OR "river*" OR "floodpl*" OR "restor*"→ 362 results

"flooding" AND "seedling*" AND "survival" AND ("plant*" OR "vegetation") → 187 results → refined with "ripar*" OR "stream*" OR "river*" OR "floodpl*" OR "restor*" → 80 results

"flooding" AND "survival*" AND ("plant*" OR "vegetation") → 706 results → refined with "ripar*" OR "stream*" OR "river*" OR "floodpl*" OR "restor*"→ 315 results

Subq. 4: Flooding effects on riparian plant species richness
"flooding" AND ("species richness" OR "species number" OR "species abundance" OR "species diversity") AND ("plant*" OR "vegetation") → 322 results → refined with "ripar*" OR "stream*" OR "river*" OR "floodpl*" OR "restor*"→ 225 results

Table S4.2. Papers used in meta-analysis survival.

Seedling survival

Chen FQ, Xie ZQ (2009) Survival and growth responses of *Myricaria laxiflora* seedlings to summer flooding. Aquatic Botany, **90**, 333-338.

Fraser LH, Karnezis JP (2005) A comparative assessment of seedling survival and biomass accumulation for fourteen wetland plant species grown under minor water-depth differences. Wetlands, **25**, 520-530.

Gladwin DN, Roelle JW (1998) Survival of plains cottonwood (*Populus deltoides* subsp. *monilifera*) and saltcedar (*Tamarix ramosissima*) seedlings in response to flooding. Wetlands, **18**, 669-674.

Lenssen JPM, ten Dolle GE, Blom CWPM (1998) The effect of flooding on the recruitment of reed marsh and tall forb plant species. Plant Ecology, **139**, 13-23.

Nabben RHM, Blom CWPM, Voesenek LACJ (1999) Resistance to complete submergence in Rumex species with different life histories: the influence of plant size and light. New Phytologist, **144**, 313-321.

Natale E, Zalba SM, Oggero A, Reinoso H (2010) Establishment of *Tamarix ramosissima* under different conditions of salinity and water availability: Implications for its management as an invasive species. Journal of Arid Environments, **74**, 1399-1407.

Sakio H (2010) Effects of flooding on growth of seedlings of woody riparian species. Journal For Research, **10**, 341-346.

Klimesova J (1994) The effects of timing and duration of floods on growth of young plants of *Phalaris arundinacea L*. and *Urtica dioica L*.: an experimental study. Aquatic Botany, **48**, 21-29.

Tallent-Halsell NG, Walker LR (2002) Responses of *Salix gooddingii* and *Tamarix ramosissima* to flooding. Wetlands, **22**, 776-785.

Adult plant survival

Banach K, Banach AM, Lamers LPM, de Kroon H, Bennicelli RP, Smits AJM, Visser EJW (2009) Differences in flooding tolerance between species from two wetland habitats with contrasting hydrology: implications for vegetation development in future floodwater retention areas. Annals of Botany, **103**, 341-351.

Lenssen JPM, van de Steeg HM, de Kroon H (2004) Does disturbance favour weak competitors? Mechanisms of changing plant abundance after flooding. Journal of Vegetation Science, **15**, 305-314.

Lockhart BR, Gardiner ES, Leininger TD, Hamel PB, Connor KF, Devall MS, Schiff NM, Wilson AD (2012) *Lindera melissifolia* responses to flood durations and light regimes suggest strategies for recovery and conservation. Plant Ecology, **214**, 893-905.

Lowe BJ, Watts RJ, Roberts J, Robertson A (2010) The effect of experimental inundation and sediment deposition on the survival and growth of two herbaceous riverbank plant species. Plant Ecology, **209**, 57-69.

Nabben RHM, Blom CWPM, Voesenek LACJ (1999) Resistance to complete submergence in Rumex species with different life histories: the influence of plant size and light. New Phytologist, **144**, 313-321.

Schaff SD, Pezeshki SR, Shields FD (2002) Effects of pre-planting soaking on growth and survival of black willow cuttings. Restoration Ecology, **10**, 267-274.

Stoecker MA, Smith M, Melton ED (1995) Survival and aerenchyma development under flooded conditions of *Boltonia decurrens*, a threatened floodplain species and *Conyza canadensis*, a widely distributed competitor. American Midland Naturalist, **134**, 117-126.

Van der Sman AJM, Joosten NN, Blom CWPM (1993) Flooding regimes and life-history characteristics of short-lived species in river forelands. Journal of Ecology, **81**, 121-130.

Voesenek LACJ, van der Sman AJM, Harren FJM, Blom CWPM (1992) An amalgamation between hormone physiology and plant ecology: a review on flooding resistance and ethylene. Journal of Plant Growth Regulation, **11**, 171-188.

Table S4.3. Papers used in meta-analysis biomass.

Asamoah SA, Bork EW (2010) Drought tolerance thresholds in cattail (*Typha latifolia*): a test using controlled hydrologic treatments. Wetlands, **30**, 99-110.

Banach K, Artur M, Lamers LPM, de Kroon H, Bennicelli RP, Smits AJM, Visser EJW (2009) Differences in flooding tolerance between species from two wetland habitats with contrasting hydrology: implications for vegetation development in future floodwater retention areas. Annals of Botany, **103**, 341–351.

Chen H, Qualls RG, Miller GC (2002) Adaptive responses of *Lepidium latifolium* to soil flooding: biomass allocation, adventitious rooting, aerenchyma formation and ethylene production. Environmental and Experimental Botany, **48**, 119-128.

Fraser LH, Karnezis JP (2005) A comparative assessment of seedling survival and biomass accumulation for fourteen wetland plant species grown under minor water-depth differences. Wetlands, **25**, 520-530.

Hussner A, Meyer A, Busch J (2008) The influence of water level and nutrient availability on growth and root system development of *Myriophyllum aquaticum*. Weed Research, **49**, 73-80.

Kercher SM, Zedler JB (2004) Flood tolerance in wetland angiosperms: a comparison of invasive and noninvasive species. Aquatic Botany, **80**, 89-102.

Klimesova J (1994) The effects of timing and duration of floods on growth of young plants of *Phalaris arundinacea L*. and *Urtica dioica* L.: an experimental study. Aquatic Botany, **48**, 21-29.

Li S, Martin LT, Pezeshki SR, Shields FD (2005) Responses of black willow (*Salix nigra*) cuttings to simulated herbivory and flooding. Acta Oecologica, **28**, 173-180.

Li S, Pezeshki SR, Goodwin S (2004) Effects of soil moisture regimes on photosynthesis and growth in cattail (*Typha latifolia*). Acta Oecologica, **25**, 17-22.

Li S, Pezeshki SR, Shields FD (2006) Partial flooding enhances aeration in adventitious roots of black willow (Salix nigra) cuttings. Journal of Plant Physiology, **163**, 619-628.

Luo FL, Nagel KA, Scharr H, Zeng B, Schurr U, Matsubara S (2011). Recovery dynamics of growth, photosynthesis and carbohydrate accumulation after de-submergence: a comparison between two wetland plants showing escape and quiescence strategies. Annals of Botany, **107**, 49-63.

Nabben RHM, Blom CWPM, Voesenek LACJ (1999) Resistance to complete submergence in Rumex species with different life histories: the influence of plant size and light. New Phytologist, **144**, 313-321.

Nakai A, Yurugi Y, Kisanuki H (2009) Growth responses of *Salix gracilistyla* cuttings to a range of substrate moisture and oxygen availability. Ecological Research, **24**, 1057–1065.

Nakai A, Yurugi Y, Kisanuki H (2010) Stress responses in *Salix gracilistyla* cuttings subjected to repetitive alternate flooding and drought. Trees, **24**, 1087-1095.

Natale E, Zalba SM, Oggero A, Reinoso H (2010) Establishment of *Tamarix ramosissima* under different conditions of salinity and water availability: Implications for its management as an invasive species. Journal of Arid Environments, **74**, 1399-1407.

Pezeshki SR, Anderson PH, Shields FD (1998) Effects of soil moisture regimes on growth and survival of black willow (*Salix nigra*) posts (cuttings). Wetlands, **18**, 460-470.

Romanello GA, Chuchra-Zbytniuk KL, Vandermer JL, Touchette BW (2008) Morphological adjustments promote drought avoidance in the wetland plant *Acorus americanus*. Aquatic Botany, **89**, 390-396.

Sakio H (2005) Effects of flooding on growth of seedlings of woody riparian species. Journal For Research, **10**, 341-346.

Smith M, Moss JS (1998) An experimental investigation, using stomatal conductance and fluorescence of the flood sensitivity of *Boltonia decurrens* and its competitors. Journal of Applied Ecology, **35**, 553-561.

Visser EJW, Bogemann GM, van de Steeg HM, Pierik R, Blom CWPM (2000) Flooding tolerance of Carex species in relation to field distribution and aerenchyma formation. New Phytologist, **128**, 93-103.

Tallent-Halsell NG, Walker LR (2002) Responses of *Salix gooddingii* and *Tamarix ramosissima* to flooding. Wetlands, **22**, 776-785.

Table S4.4. Morphological adjustments to flooding stress, respective authors and the number of papers in which the trait was explanatory for response success.

Plant trait	Author	Trait explanatory for response success during flooding (number of papers from a total of 39)
Increase shoot biomass / shoot elongation	Asamoah & Bork, 2010+; Banach et al., 2009+; Hussner et al., 2008+; Kercher et al., 2004+, Klimesova, 1994; Lowe et al., 2010+; Smith & Moss, 1998+; Van der Sman et al., 1993+; Visser et al., 2000+; Voesenek et al., 1992+.	9
Aerenchyma development / increased root porosity	Chen et al., 2002+; Chen et al., 2009*; Hussner et al., 2008+; Kercher et al., 2004+; Lenssen et al., 1998; Li et al., 2006+; Luo et al., 2011*; Nabben et al., 1999*; Pezeshki et al., 1998+; Sakio, 2005*; Smith & Moss, 1998*; Stoecker et al., 1995+; Visser et al., 2000+; Voesenek et al., 1992+.	8
Adventitious root development	Banach et al., 2009+; Chen et al., 2002+; Kercher et al., 2004+; Klimesova, 1994; Li et al., 2006; Lockhart et al., 2012*; Lowe et al., 2010*; Nabben et al., 1999*; Natale et al., 2010*; Pezeshki et al.,1998*; Sakio, 2005*; Schaff et al., 2002*; Stoecker et al., 1995; Tallent-Halsell & Walker, 2002+; Voesenek et al., 1992*.	4
Stomatal closure / increased stomatal regulation	Chen et al., 2009*; Li et al., 2004+; Nakai et al., 2010+; Pezeshki et al., 1998+; Smith & Moss, 1998+; Li et al., 2006; Nakai et al., 2009*.	4
Slowdown of growth; decrease in leaf area / reduced transpiration area	Chen et al., 2009; Luo et al., 2011; Nakai et al., 2009+; Nakai et al., 2010+; Pezeshki et al.,1998+; Van der Sman et al., 1993+.	4
Hypertrophic lenticels development	Nakai et al., 2009+, Nakai et al., 2010+; Lockhart et al., 2012*; Pezeshki et al., 1998+; Sakio, 2005*, Tallent-Halsell & Walker, 2002.	3

\+ = trait explanatory for the response success during flooding
* = trait mentioned in the paper as an important adjustment, but tested experimentally in other studies
no symbol = trait mentioned in the paper as an important adjustment

Table S4.5. Overview of species used in meta-analysis, including species names, shoot elongation ability, root porosity and respective meta-analysis study.

Species name (species involved in meta-analysis)	**Growth form** (herbaceous (annual/perennial/biennial), helophyte, grass, shrub, tree species)	**Shoot elongation** (1=yes, 0=no, n.d.=no data available)	**Root porosity** (response ratio, n.d=no data available)	**Meta-analysis study** (a=adult survival, b=biomass, s=seedling survival
Achillea millefolium	herb (p)	0	1.222	a,b
Acorus americanus	herb (p)	n.d.	n.d.	b
Aesculus turbinata	tree	n.d.	n.d.	b,s
Agrostis stolonifera	grass	n.d.	n.d.	a
Alternanthera philoxeroides (Mart.) Griseb.	herb (p)	n.d.	n.d.	b
Arabidopsis suecica	herb (a)	n.d.	n.d.	a,b
Arrhenatherum eliatus	grass	n.d.	n.d.	a
Asclepias incarnata	herb (p)	0	0.947	b
Aster ontarionis	herb (p)	n.d.	n.d.	b
Aster pilosus	herb (p)	n.d.	n.d.	b
Bidens cernua	herb (a)	1	0.730	b
Boltonia decurrens	herb (p)	n.d.	n.d.	a,b
Bromus ciliatus	grass	0	n.d.	b
Calamagrostis canadensis	grass	1	1,333	b
Calamagrostis canadensis (Michx.) Beauv.	grass	n.d.	n.d.	b,s
Calotis scapigera	herb (p)	n.d.	n.d.	a
Carex bichenoviana	helo	n.d.	n.d.	a
Carex davalliana	helo	0	2.234	b
Carex ferruginea	helo	0	3.950	b
Carex granularis	helo	0	0.756	b
Carex limosa	helo	1	5.696	b

Carex lurida Wahlenb.	helo	n.d.	n.d.	b,s
Carex nigra	helo	0	n.d.	b
Carex rostrata	helo	0	1.757	b
Carex sempervirens	helo	0	5.839	b
Carex stipata Hudson	helo	n.d.	n.d.	b,s
Carex stricta	helo	0	2.350	b
Carex tribuloides Wahlenb.	helo	n.d.	n.d.	b,s
Carex vulpinoidea Michx.	helo	n.d.	n.d.	b,s
Cerastium fontanum	herb (a/p)	n.d.	n.d.	a,b
Cercidiphyllum japonicum	tree	n.d.	n.d.	b,s
Chenopodium rubrum	herb (a)	1	n.d.	a
Cirsium arvense	herb (p)	0	1.306	s
Conyza canadensis	herb (a)	n.d.	n.d.	a,b
Deschampsia cespitosa	grass	n.d.	2.043	a,b
Elymus virginicus L.	grass	n.d.	n.d.	s
Elytrigia repens	grass	n.d.	n.d.	a
Epilobium hirsutum	herb (p)	1	1.000	s
Eupatorium cannabinum	herb (p)	0	1.214	s
Eupatorium maculatum	herb (p)	0	7.000	b
Eupatorium perfoliatum	herb (p)	0	0.793	b
Fraxinus platypoda	tree	n.d.	n.d.	b,s
Galium boreale	herb (p)	n.d.	n.d.	a,b
Galium palustre	helo		1.571	a,b
Glyceria canadensis (Michx.) Trin.	helo	n.d.	n.d.	b,s
Glyceria striata	grass	0	1.105	b
Helianthus grosseserratus	herb (p)	0	n.d.	b

Table S4.5. Continued

Species name (species involved in meta-analysis)	**Growth form** (herbaceous (annual/perennial/biennial), helophyte, grass, shrub, tree species)	**Shoot elongation** (1=yes, 0=no, n.d.=no data available)	**Root porosity** (response ratio, n.d=no data available)	**Meta-analysis study** (a=adult survival, b=biomass, s=seedling survival
Hemarthria altissima (Poir.) Stapf & C.E	grass	n.d.	n.d.	b
Holcus lanatus	grass	0	2.000	a,b
Lepidium latifolium	herb (p)	n.d.	1.087	b
Linaria vulgaris	herb (p)	n.d.	n.d.	a,b
Lindera melissifolia	shrub (p)	n.d.	n.d.	a
Lolium perenne	grass	n.d.	1.960	a,b
Lycopus europaeus	helo	0	1.140	s
Lythrum salicaria L.	helo	1	8.540	b,s
Mentha aquatica	helo	0	1.505	s
Mimulus ringens L.	herb (p)	n.d.	n.d.	b,s
Myositis scorpioides	helo	0	1.610	s
Myricaria laxiflora	shrub (p)	n.d.	n.d.	s
Myriophyllum aquaticum	herb (p, submerged)	n.d.	1.333	b
Oligoneuron riddellii	herb (p)	0	0.441	b
Phalaris arundinacea	helo	1	1.168	b,s
Phleum pratense	grass	n.d.	1.308	a,b
Plantago lanceolata	herb (p)	n.d.	n.d.	a,b
Plantago major	herb (p)	1	n.d.	a,b
Poa trivialis	grass	n.d.	n.d.	a
Populus deltoides subsp. monilifera	tree	n.d.	n.d.	s
Prunella vulgaris	herb (p)	n.d.	n.d.	a,b

Pterocarya rhoifolia	tree	n.d.	n.d.	b,s
Pterostyrax hispida	tree	n.d.	n.d.	b,s
Quercus mongolica var. grosseserrata	tree	n.d.	n.d.	b,s
Ranunculus acris	herb (p)	1	2.032	a,b
Rumex acetosa	herb (p)	0	n.d.	a,b
Rumex confertus	herb (p)	n.d.	1.029	a,b
Rumex crispus	herb (p)	1	2.648	a,b
Rumex maritimus	herb (a/p)	1	3.000	a,b,s
Rumex orbiculatus A. Gray	herb (p)	n.d.	n.d.	b,s
Rumex palustris	herb (a/b/p)	1	1.772	a,b,s
Rumex thyrsiflorus	herb (p)	1	n.d.	a,b,s
Salix gooddingii	tree	n.d.	n.d.	b,s
Salix gracilistyla	tree	n.d.	n.d.	b
Salix nigra	tree	n.d.	0.478	a,b
Scirpus cyperinus (L.) Kunth.	herb (p)	n.d.	n.d.	b,s
Silene pratensis	herb (a/b/p)	n.d.	n.d.	a,b
Solidago gigantea	herb (p)	0	1.214	b
Spartina pectinata-K	grass	0	2.296	b
Spartina pectinata-S	grass	0	1.550	b
Symphyotrichum puniceum	herb (p)	0	1.226	b
Tamarix ramosissima	tree	n.d.	n.d.	b,s
Typha latifolia	helo	0	0.963	b
Urtica dioica	herb (p)	n.d.	n.d.	b,s
Verbascum densiflorum	herb (b/p)	n.d.	n.d.	a,b
Verbesina alternifolia (L.) Britt.	herb (p)	n.d.	n.d.	s
Zizania aquatica L.	grass	n.d.	n.d.	b, s

Table S4.6. Papers on species richness and composition.

Baattrup-Pedersen A, Friberg N, Larsen SE, Riis T (2005) The influence of channelisation on riparian plant assemblages. Freshwater Biology, 50, 1248–1261.

Baattrup-Pedersen A, Dalkvist D, Dybkjær JB, Riis T, Larsen SE, Kronvang B (2013a) Species recruitment following flooding, sediment deposition and seed addition in restored riparian areas. Restoration Ecology, 21, 399-408.

Baattrup-Pedersen A, Jensen KMB, Thodsen H, Andersen HE, Andersen PM, Larsen SE, Riis T, Andersen DK, Audet J, Kronvang B (2013b) Effects of stream flooding on the distribution and diversity of groundwater-dependent vegetation in riparian areas. Freshwater Biology, 58, 817-827.

Beltman B, Willems JH, Güsewell S (2007) Flood events overrule fertiliser effects on biomass production and species richness in riverine grasslands. Journal of Vegetation Science, 18, 625-634.

Capon SJ (2005) Flood variability and spatial variation in plant community composition and structure on a large arid floodplain. Journal of Arid Environments, 60, 283–302.

Decocq G (2002) Patterns of plant species and community diversity at different organization levels in a forested riparian landscape. Journal of Vegetation Science, 13, 91-106.

Gerard M, El Kahloun M, Rymen J, Beauchard O, Meire P (2008) Importance of mowing and flood frequency in promoting species richness in restored floodplains. Journal of Applied Ecology, 45, 1780-1789.

Horner GJ, Cunningham SC, Thomson JR, Baker PJ, Mac Nally R (2012) Forest structure, flooding and grazing predict understorey composition of floodplain forests in southeastern Australia. Forest Ecology and Management, 286, 148-158.

Hughes JW, Cass WB (1997) Pattern and Process of a Floodplain Forest, Vermont, USA: Predicted Responses of Vegetation to Perturbation. Journal of Applied Ecology, 43, 594-612.

Jansson R, Zinko U, Merritt DM, Nilsson C (2005) Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. Journal of Ecology, 93, 1094-1103.

Johansson ME, Nilsson C (2002) Responses of riparian plants to flooding in free-flowing and regulated boreal rivers: an experimental study. Journal of Applied Ecology, 39, 971-986.

Lyon J, Sagers CL (1998) Structure of herbaceous plant assemblages in a forested riparian landscape. Plant Ecology, 138, 1-16.

Petit NE, Froend RH, Davies PM (2001) Identifying the natural flow regime and the relationship with riparian vegetation for two contrasting western Australian rivers. Regulated Rivers: Research and Management, 17, 201-215.

Renöfält BM, Merritt DM, Nilsson C (2007) Connecting variation in vegetation and stream flow: the role of geomorphic context in vegetation response to large floods along boreal rivers. Journal of Applied Ecology, 44, 147-157.

Ström L, Jansson R, Nilsson C (2012) Projected changes in plant species richness and extent of riparian vegetation belts as a result of climate-driven hydrological change along the Vindel River in Sweden. Freshwater Biology, 57, 49-60.

Ström L, Jansson R, Nilsson C, Johansson ME, Xiong S (2011) Hydrologic effects on riparian vegetation in a boreal river: an experiment testing climate change predictions. Global Change Biology, 17, 254-267.

Stromberg JC, Beauchamp VB, Dixon MD, Lite SJ, Paradzick C (2007) Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid southwestern United States. Freshwater Biology, 52, 651-679.

Stromberg JC, Hazelton AF, White MS (2009) Plant species richness in ephemeral and perennial reaches of a dryland river. Biodiversity and Conservation, 18, 663-677.

Tabacchi E (1995) Structural variability and invasions of pioneer plant communities in riparian habitats of the middle Adour River (SW France). Canadian Journal of Botany, 73, 33-44.

Toogood SE, Joyce CB (2009) Effects of raised water levels on wet grassland plant communities. Applied Vegetation Science, 12, 283–294.

Townsend PA (2001) Relationships between vegetation patterns and hydroperiod on the Roanoke River floodplain, North Carolina. Plant Ecology, 156, 43–58.

Wassen MJW, Peeters WHM, Olde Venterink H (2003) Patterns in vegetation, hydrology, and nutrient availability in an undisturbed river floodplain in Poland. Plant Ecology, 165, 27-43.

Table S4.7. Summary of the main effects of flooding on riparian plant species richness and composition, organised according to the main trends in species declines

Main trend	Authors	Main effect of increased flooding on species richness	Observations	Mechanisms	Bio-geographical region	Research set-up
DECREASE SPECIES RICHNESS (9)	Baattrup-Pedersen et al,. 2013a	Shift towards more productive species stimulated by flooding	Compositional changes in vegetation, shifts towards more productive species in areas previously dominated by low and intermediately productive species. Flooding and sediment deposition play a limited role for recruitment of target species.	Sediment deposition enhanced by flooding may entail a risk of losing diversity in riparian areas.	Atlantic, Denmark	Restored riparian areas investigated more prone to flooding. Role of flooding, sediment deposition and seed addition investigated.
	Baattrup-Pedersen et al., 2013b	Higher species richness in low frequency flooded rich fens compared to higher frequency flooded fens.	Percentage of stress-tolerant species higher in low intensity flooded areas than in high intensity flooded areas.	Higher species richness in low frequency flooded fens may be caused by competitive release.	Atlantic, Denmark	Effects of frequency and duration of flooding investigated at four sites.
	Beltman et al., 2007	Extreme winter floods led to a reduction of species richness and increased biomass production.	Reduction in species richness (from ca. 24 to 15 species) and an increase in biomass production.	Lower species richness may result from the promotion of highly competitive species: first tall forbs and later graminoids.	Atlantic, the Netherlands	Fertilisation experiment (21 years), recording species composition, vegetation biomass and nutrient concentrations, also including the effects of two major winter flood events.

Table S4.7. Continued

Main trend	Authors	Main effect of increased flooding on species richness	Observations	Mechanisms	Bio-geographical region	Research set-up
	Decocq, 2002	Flooding-induced disturbances result in low plant species diversity.	High species densities are suppressed by flooding, most productive habitats were also found here.	Flooding-induced disturbances (stressful environments) result in low plant species diversity. Moderate flooding-induced disturbance enhances herb species richness.	Atlantic, Belgium and France	Description of the structure of vascular vegetation diversity along a forested riparian landscape, applying integrated synusial phytosociology combined with traditional measures of diversity.
	Petit et al., 2001	An increase in duration and frequency of flooding reduced species richness and cover of shrubs in river with stable yearly discharge, while flooding regime had no impact on river with seasonality of flows.	Water depth, duration of flood events and the number of flood events per year show a significant correlation with aspects of the riparian vegetation.	Response of riparian vegetation is strongly dependent on natural flow regime.	Semi-arid / subtropical, SW and NW Australia	Analysis of long-term flow data in relationship with species richness and cover of river riparian vegetation along the Blackwood river (discharge stable) and Ord river (strong seasonality of flows)
	Renöfalt et al., 2007	Extreme floods reduced riparian plant species richness in tranquil reaches.	Extreme floods reduced riparian plant species richness in tranquil reaches, while species richness in turbulent reaches remained constant.	Tranquil reaches may become more anoxic during floods because of fine-grade soils than turbulent reaches, which leads to higher plant mortality.	Boreal, northern Sweden	Surveys of plant species richness conducted after a significant flooding and a period of more moderate flooding.

	Ström et al., 2011	Loss of species richness, shift in species composition.	Riparian vegetation from the highest elevation transplanted to lower elevation increased in biomass and decreased in species richness.	Flood duration played a strong role in structuring riparian plant community organisation.	Boreal, northern Sweden	Transplantation field experiment with turfs transplanted lower down the floodplain to simulate flooding conditions, monitored over 6 years.
	Ström et al., 2012	Reduction of the most species-rich belts, resulting in an overall decline in species richness.	The graminoid belt below the shrub belt is predicted to shift upwards in elevation, while the amphibious vegetation belt at the bottom of the riparian zone increases in size.	Strong role of flood duration in structuring riparian plant species composition.	Boreal, northern Sweden	Quantification of effects predicted for hydrological change (increased spring floods, summer droughts) on riparian plant species richness, using different scenarios.
	Wassen et al., 2003	Species richness increases and standing crop decreases from the river towards the margin.	Flood variables explained best absence and presence of species and variation in species composition.	Impact of hydrology and nutrient release.	Continental, NE Poland	Comparison of vegetation composition with site factors such as flood duration and inundation depth during spring floods.
INCREASE SPECIES RICHNESS (7)	Baattrup-Pedersen et al., 2005	Alpha diversity sign. higher along natural streams, prone to flooding.	Flooding plays a key role in maintaining high levels of diversity.	Flooding may create and sustain a wide range of habitats by creating temporarily and spatially complex environmental gradients.	Atlantic, Denmark	Comparison of diversity in natural mid-sized lowland streams and channelised parts.
	Capon, 2005	Flooding increases species richness, total cover and cover amongst major plant groups.	Flooding plays an important role in maintaining spatial heterogeneity in plant community composition and structure.	Flow variability promotes landscape heterogeneity.	Arid / Semi-arid, Central Australia	Comparison of sites with a different flood frequency.

Table S4.7. Continued

Main trend	Authors	Main effect of increased flooding on species richness	Observations	Mechanisms	Bio-geographical region	Research set-up
	Horner et al., 2012	Flooding was positively associated with native species richness.	Flooded stands contained twice the number of native species found in un-flooded stands.	Germination of flood-dependent species from the soil seed bank and the persistence of the native flora.	Semi-arid and mesic, SE Australia.	Field survey to examine potential drivers of species richness and composition.
	Hughes & Cass, 1997	Flooding regime defined the composition and distribution of the standing vegetation at different distances from the stream.	The highest seedbank species richness occurred 5 m from the stream, while species richness of the standing flora was constant (4-6 species) 5, 15 and 25 m from the stream.	Flood-induced disturbance generates a highly diverse mosaic of possible floras.	Continental, Vermont, USA	Evaluation of the potential diversity of vegetation in a lowland floodplain forest. Quantification and comparison between potential floras (newly fallen seeds, seed bank and seeds transported by water) with the standing flora.
	Jansson et al., 2005	Flooding increased the number of colonising species, potential species richness.	Hydrochory increased with flooding and resulted in more diverse plant communities after 3 years of succession.	Long-distance dispersal increases with flooding. Plant dispersal by water and fluvial disturbance enhance species richness.	Boreal, northern Sweden	Comparison of colonization in flooded and non-flooded plots.
	Stromberg et al., 2007	Frequent flooding results in higher plant species diversity and an abundance of pioneer wetland plant species.	Patch diversity, riparian plant species diversity and abundance of flood-dependent wetland tree species are enhanced by increasing flood frequency.	Increases in water availability and ecosystem disturbance positively influence diversity along perennial streams.	Desert, Arizona	Year-round survey of several reference rivers in Arizona's Sonoran Desert region.

	Stromberg et al., 2009	Species richness at ephemeral-flow sites increased during flooding periods.	During seasons with elevated stream flows, species richness at ephemeral-flow sites increased to levels at or slightly above those of perennial-flow sites.	Moderate flooding stimulated establishment of opportunistic species (mainly annuals) during the wet season.	Desert, SE Arizona, USA	Comparison between sites with perennial stream flow and ephemeral stream flow over a 2 year period spanning drought and wetter conditions.
NO SIGN. DIFFERENCE (2)	Gerard et al., 2008	No significant differences in realised species richness in vegetation of flooded and non-flooded meadows.	Seed densities in flooded meadows significantly higher than in non-flooded meadows, seed banks of flooded meadows contained more hydrochorous species, but no difference in realised species richness.	Despite higher input of seeds during flooding, it does not substantially enhance potential species richness due to impeding factors.	Atlantic, Belgium.	Comparison seed bank and vegetation composition of flooded and non-flooded semi-natural meadows.
	Toogood & Joyce, 2009	No significant changes in diversity metrics associated with raised water levels.	With increasing wetness, sites were characterised by more bare ground and wetland plants and species with a stress-tolerating competitive strategy.	Composition of grassland plant communities responds to raised water levels.	Atlantic, southeast England, UK.	Comparison of grasslands with shallow inundation (<8 cm) and relatively short inundation duration (<3 months) and sites with deeper and prolonged flooding.
NO RESULTS RICHNESS but composition or performance (4)	Johansson & Nilsson, 2002	Flood duration and frequency reduced performance (growth and survival) in all species and during all time periods.	Regulated stream regimes had a negative relation with plant performance, while free-flowing regime variables had a positive relation.	Strong changes in the water level regime had negative effects on performance of individual plant species.	Boreal, northern Sweden	Comparison of four riparian plant species (Betula pubescens, Carex acuta, Filipendula ulmaria, Leontodon autumnalis) over 2 years at four free-flowing and four regulated riverbank sites in northern Sweden.

Table S4.7. Continued

Main trend	Authors	Main effect of increased flooding on species richness	Observations	Mechanisms	Bio-geographical region	Research set-up
	Lyon & Sagers, 1998	Flooding stimulates species replacement.	At the lower elevations most prone to flooding, the herb layer showed a high species replacement rate	Disturbance caused by flooding at the lower elevations (0-3 m).	Continental, Missouri, USA.	Assessment of patterns of herbaceous and woody species richness, plant-environment interactions and correspondence between the herb and tree layer.
	Tabacchi,1995	Increase in hygrophilous species in the oldest arms of the river.	Plots located in the oldest arms of the river channels showed greatest sensitivity to flooding conditions compared to those located in younger zones.	High variation in mean daily discharge between a normal year, a wet yea, and a dry year.	Atlantic, SW France	Pioneer vegetation, changes in space and time measured. Normal (1987), wet (1988) and a dry year (1989).
	Townsend, 2001	Strong indication that inundation during extremely wet years controls species composition.	Wet conditions correlated most strongly with Detrended Correspondence Analysis axis 1, indicating that inundation controls species composition.	Spring hydroperiod is an important mechanism that may drive competitive sorting along the flooding gradient.	Subtropical, North Carolina, USA.	Vegetation surveys and spatial data, combined with a flood simulation model. Detrended correspondence analysis.

Chapter 5

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

Annemarie G. Garssen, Annette Baattrup-Pedersen, Tenna Riis, Bart M. Raven, Carl C. Hoffman, Jos T. A. Verhoeven and Merel B. Soons

Global Change Biology (2017), 23, 3052–3063
doi: 10.1111/gcb.13687

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.

Introduction

The magnitude and frequency of intense precipitation events are expected to increase in many parts of the world in the near future (Bates et al., 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 & Decamps, 1997; Poff et al., 1997; Merritt et al., 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 et al., 1991; Naiman & Decamps, 1997; Naiman et al., 2005; Verry et al., 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 & Decamps, 1997; Naiman et al., 1993; Richardson et al., 2007; Verhoeven et al., 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 et al., 2015a; Silvertown et al., 1999; Ström et al., 2011) and on the differential arrival of plant seeds with rising and falling water levels (Fraaije et al., 2015b; 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 et al., 2015a; Fraaije et al., 2015b; 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; Decamps, 1993), resulting in changes in their hydrology and, subsequently, their vegetation (Garssen et al., 2015; Garssen et al., 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 et al., 2015a; Fraaije et al., 2015b; Garssen et al., 2015; Van Eck et al., 2005; Van Eck et al., 2004; Voesenek et al., 2004). Seed transport by water is an important dispersal mechanism in riparian zones (Moggridge & Gurnell, 2010; Moggridge et al., 2009), which contributes to species sorting along the hydrological gradient (Fraaije et al., 2015b; 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 et al., 2002; Fraaije et al., 2015b; Fraaije et al., 2015b; Garssen et al., 2015; Lenssen & de Kroon, 2005; Visser et al., 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 et al., 2009; Noe et al., 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 et al., 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 et al., 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 et al., 1998; Smolders, Lamers et al., 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 et al., 2015; Lunt et al., 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 (Fig. 5.1). 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.

Materials and methods

Study sites and experimental design

Five riparian areas in Denmark, Germany and the Netherlands were selected for the flooding experiment (Fig. 5.1a). In Denmark, the riparian areas were situated along a channelized agricultural stream (Voel bæk, Fig. 5.1b) 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 located along the head reach of a restored stream (Boye, Fig. 5.1e) 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, Fig. 5.1d; Groote Molenbeek, Fig. 5.1f). 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 5.1.

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

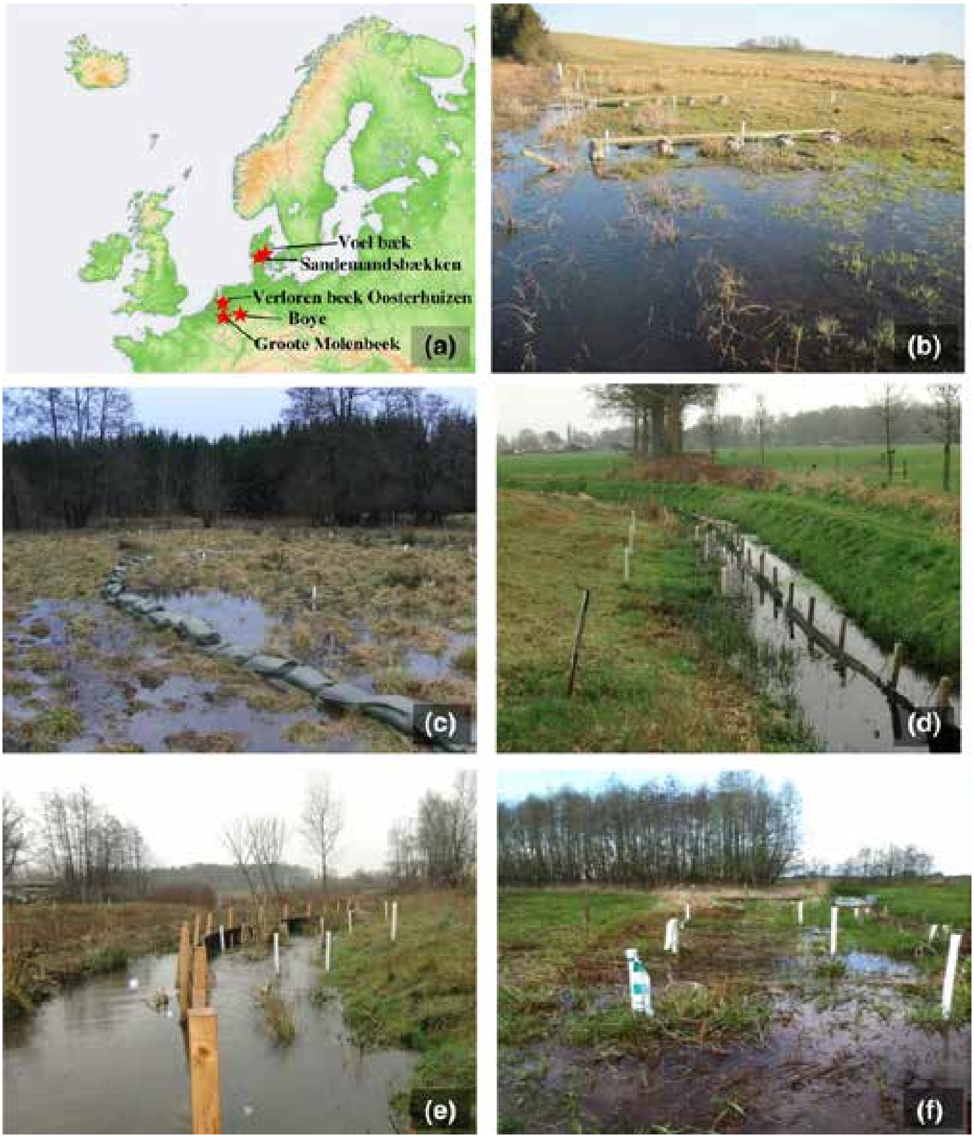


Fig. 5.1. Overview of the stream riparian wetland sites in northwestern Europe (a), with pictures of the flooding treatments: Voel bæk (Denmark) (b), Sandemandsbækken (Denmark) (c), Verloren beek Oosterhuizen (the Netherlands) (d), Boye (Germany) (e), Groote Molenbeek (the Netherlands) (f).

water level than under normal winter conditions (see S5.1). 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 5.2). 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 (Fig. 5.2), so that there were nine samples for each variable per stream section and 90 samples in total (nine samples x two sections x 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 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.

Table 5.1. Name, location, climate characteristics, catchment size and date of restoration activities of the stream riparian wetland 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
Sandemands-bækken	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 5.2. 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.

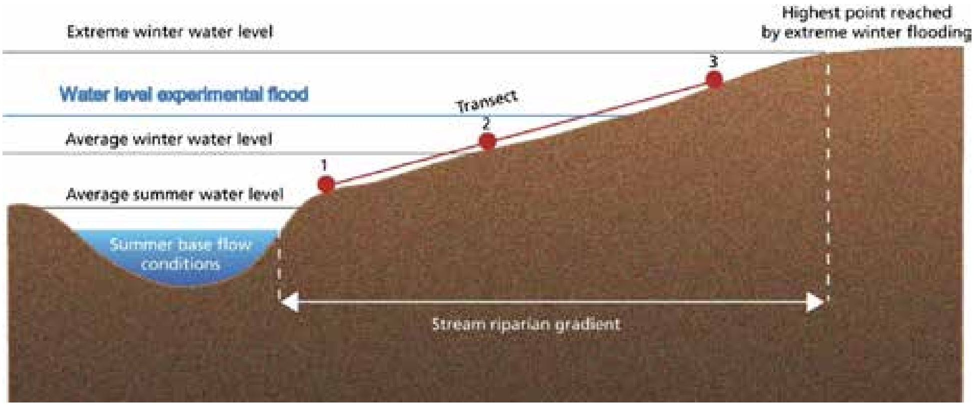


Fig. 5.2. Schematic cross section of the stream riparian gradient and location of sampling points (1 (low), 2 (middle) and 3 (high)) in relation to average water levels.

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 et al., 1954).

In the summers following the manipulated flooding periods, plant aboveground biomass at the sampling points was clipped at a 50 x 50 cm^2 plot at peak standing crop (August), oven-dried (48 hr, 70°C) and weighed. Vegetation releves were made in another, nonharvested 50 x 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 x (species loss + species gain)/(species loss + species gain + equal species; Peterson et al., 2002).

Seed traps consisting of 25 x 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 et al., 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 et al., 2015b) and identified to species level using the "Digital Seed Atlas of the Netherlands" (Cappers et al., 2006).

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 & Smilauer, 2012).

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.

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 (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; 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 ($p = .536$; Fig. 5.3a). 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 5.3). Additionally, plant species richness was negatively related to total plant biomass and plant-available N (Table 5.3, S5.3).

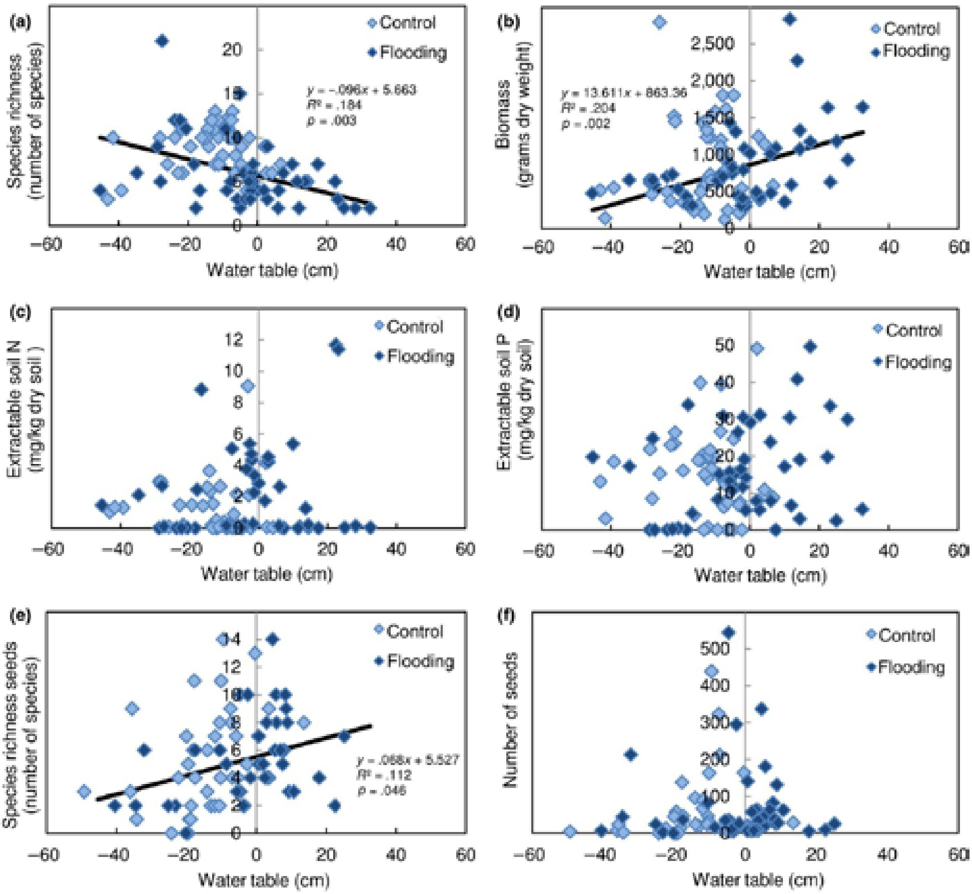


Fig. 5.3. Vegetation and soil characteristics in relation to water level in control and flooded plots along the five investigated European lowland streams: Species richness of the riparian vegetation (a), aboveground plant biomass (b), extractable soil N (c), extractable soil P (d), species richness 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.

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; Fig. 5.3b). No general relation between biomass and water level was observed, but the interaction between section and water level was significantly negative (Table 5.3), supporting the observation that there was only a positive relation between biomass and water level at the flooding sections. Furthermore, biomass was also strongly positively related to site temperature and soil extractable P (Table 5.3, S5.3).

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; Fig. 5.3c). Patterns related to extractable soil P and water levels were less clear (Fig. 5.3d). In the LMM, however, extractable soil N and P were both positively related to water level (Table 5.3, S5.3), indicating that extractable soil N and P increased following the late winter flooding treatment.

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; Fig. 5.3e; Table 5.3, S5.3). The species richness of deposited seeds was also positively related to the number of deposited seeds (p < .001 in the LMM, S5.3). No linear relation was found between the number of deposited seeds and any other variables, with the exception of temperature (Table 5.3, S5.3). The number of deposited seeds showed a clear optimum around the waterline (water levels close to zero; Fig. 5.3f), 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).

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 (Fig. 5.4). 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 (S5.4). Plant species composition for each stream individually is presented in Figure 5.5 and S5.5. 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.

Table 5.3. 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 x 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 S5.3.

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, Fig. 5.6). In all cases, 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.

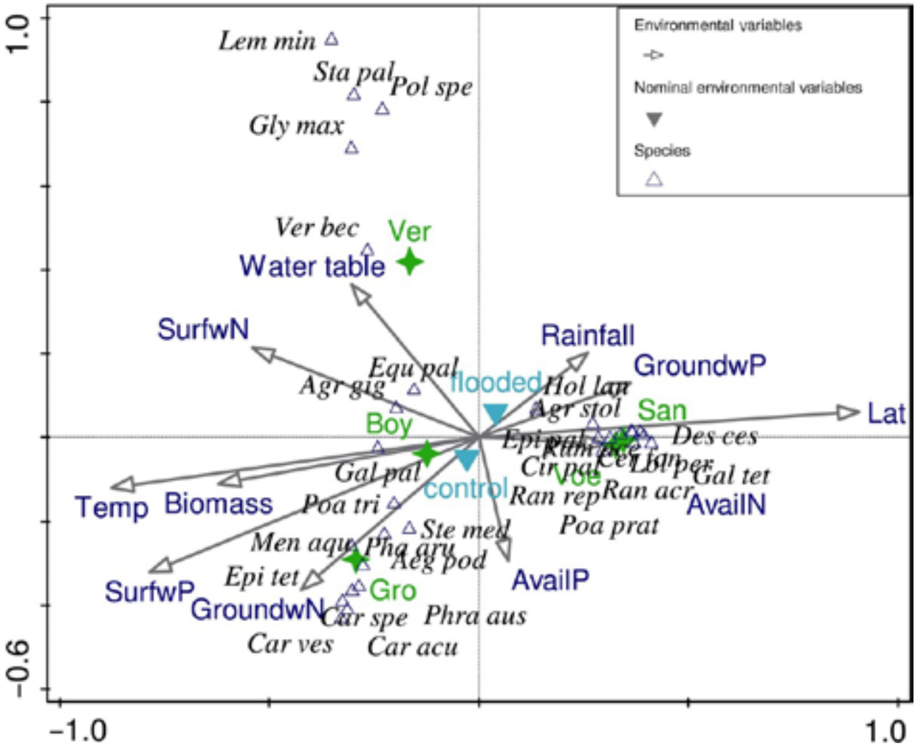


Fig. 5.4. Distribution of plant species and sites along two canonical axes at the end of the flooding experiment (2013). Abbreviations of stream names: Voe = Voel bæk, San = Sandemandsbækken, Ver = Verloren beek Oosterhuizen, Boy = Boye, Gro = Groote Molenbeek. Variables: SurfwN = N in surface water, 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 S5.5 for a complete species list.

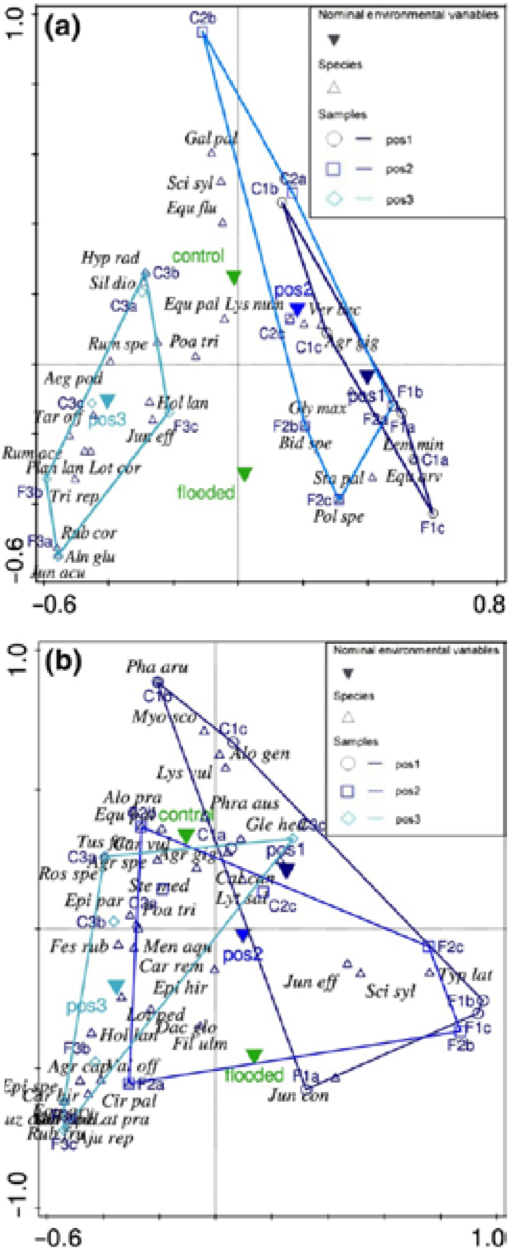


Fig. 5.5. Plant species composition at the Verloren beek Oosterhuizen (a) and Boye (b) along two canonical axes. Correspondence analyses for the other streams are given in S5.6. The first two axes are correlated with position along the stream riparian gradient (pos. 1: lowest position along gradient, 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 S5.5 for a complete species list.

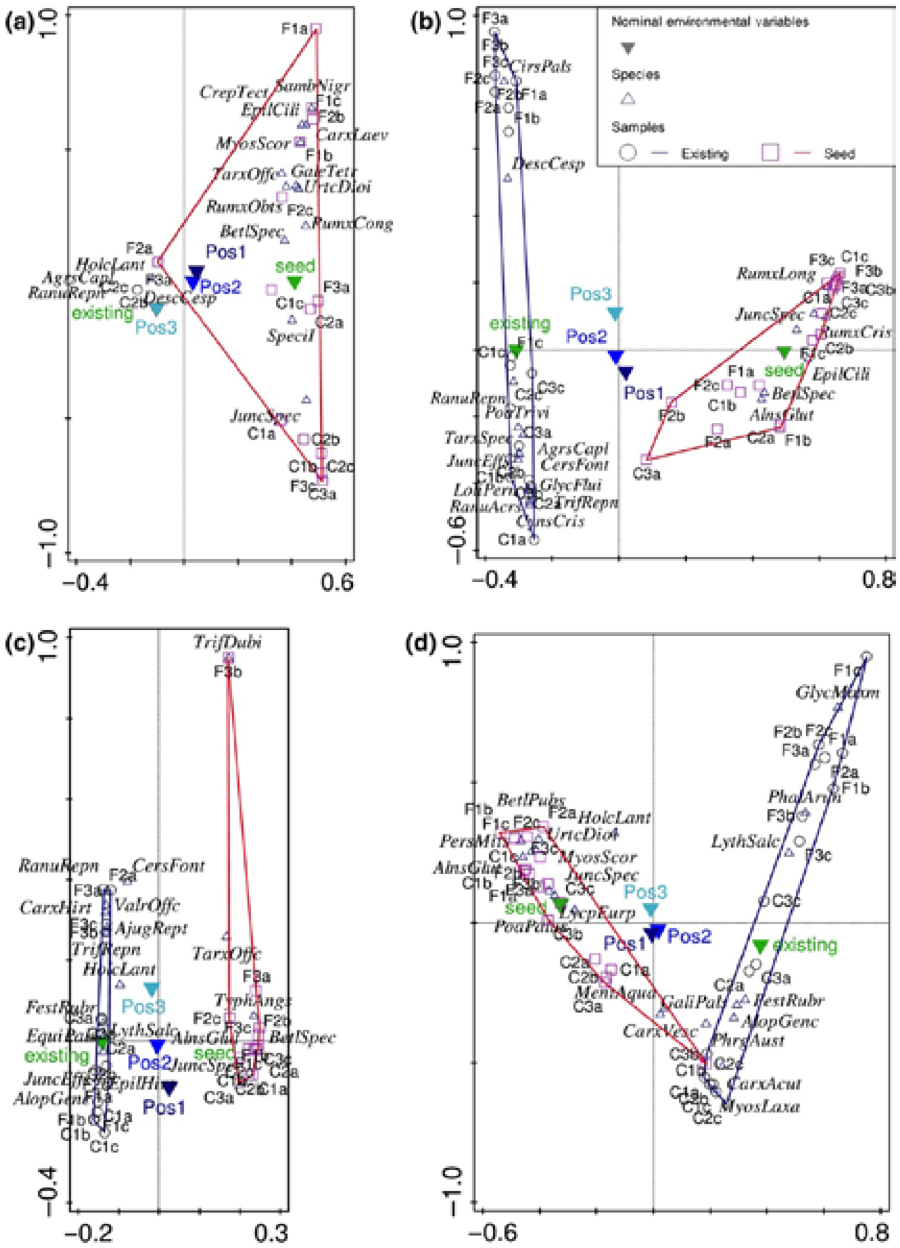


Fig. 5.6. Species composition of adult plant communities and deposited seeds at the Voel bæk (a), Sandemandsbækken (b), Boye (c) and Groote Molenbeek (d) along two canonical axes. The first two axes are correlated with position along the stream riparian gradient (pos. 1: lowest position along gradient, 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 S5.5 for a complete species list.

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).

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 et al., 1998; Hautier et al., 2009; Stevens et al., 2004; Suding et al., 2005). Particularly, the enrichment with P, via deposited sediment, is expected to increase riparian nutrient availability following flooding (Beumer et al., 2007; Walls et al., 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 et al., 2015a; Garssen et al., 2015; Sarneel & Soons, 2012; Voesenek et al., 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 et al., 2015b; Silvertown et al., 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 (S5.2). 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 et al., 2013; Brederveld et al., 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.

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 et al., 2012). This negative response may be alleviated by measures at the catchment scale (Verhoeven et al., 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).

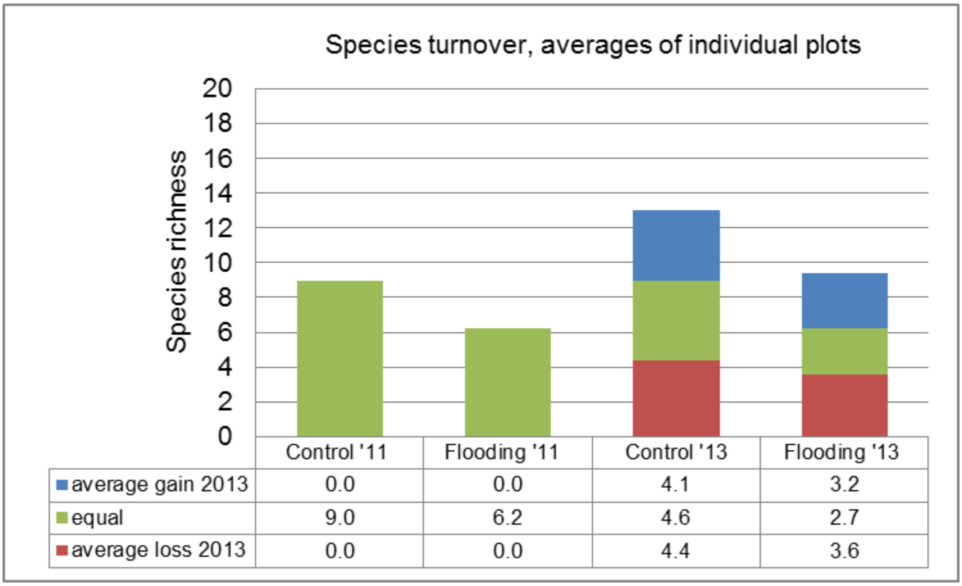
Supporting information

S5.1. Overview of general experimental design and dam constructions.

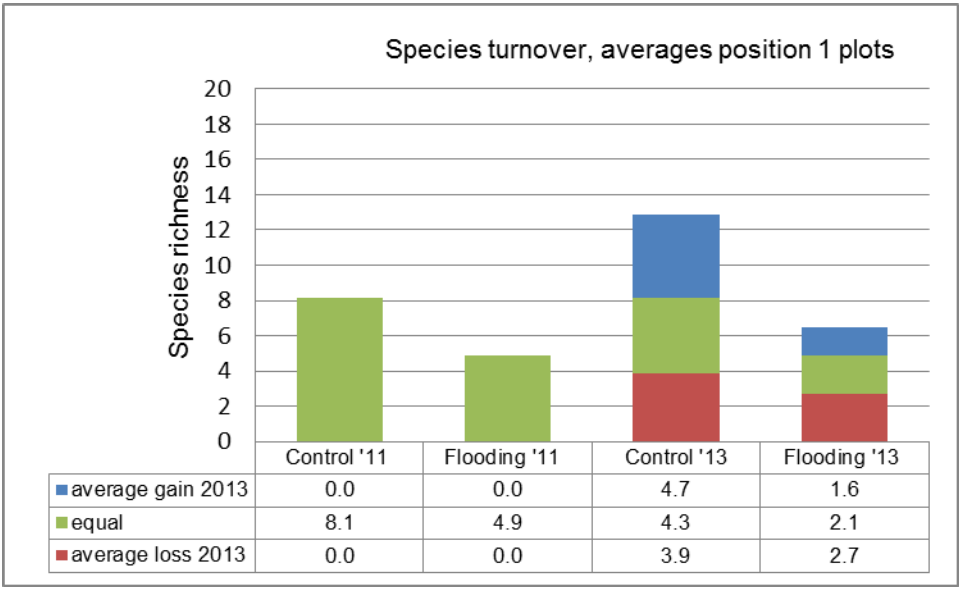
To increase surface water levels in the flooding section of each stream, discharge levels were manipulated. At the Verloren beek Oosterhuizen and Boye – relatively small lowland streams – we constructed longitudinal dams to increase water levels at one of the two shorelines in the flooding section. By diverting the water stream through approximately one fourth of the riparian streambed, we sufficiently increased discharge levels to the point of desired flooding amplitude. For the construction of the longitudinal dams, we used plates of the brand 'Trespa', which were connected to each other and attached to poles, and firmly put in the streambed. Upstream of the longitudinal dam, a so called 'beam weir' was placed. During the flooding treatment, beams were placed in the cavities of the weir, to force the water to flow through the small part of the stream. Construction details and former experiences from Verdonschot et al. (2001) were taken into account. The Danish streams (Voel bæk and Sandemandsbækken) were somewhat larger and situated in flat or gradually sloping stream valleys. Here, sand bags instead of plates were applied to create longitudinal dams to guide the stream water. At the Groote Molenbeek, the largest of the five streams, a pump was used to divert water from the main channel to the flooding section. Iron plates were stably put into the streambed close to the riparian zone, so we were able to increase water levels in the flooding section. Fig. 5.7. provides pictures of the constructions.

Figure 5.7. Longitudinal dam construction made of 'Trespa' plate material (a), a sand bag dam (b), and close-up of pump installation at the boundary of the flooding section (c).

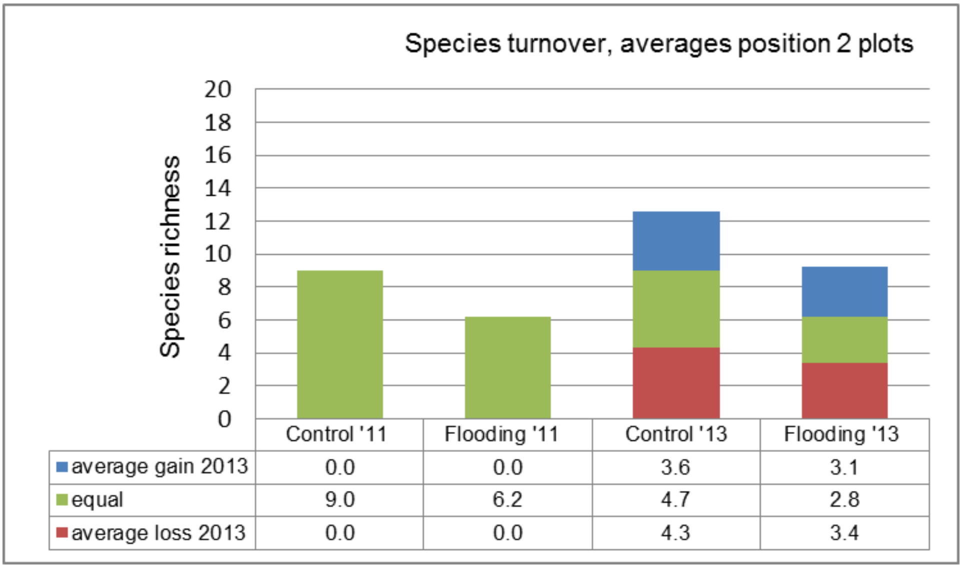
S5.2. Species turnover along the five investigated stream riparian gradients.



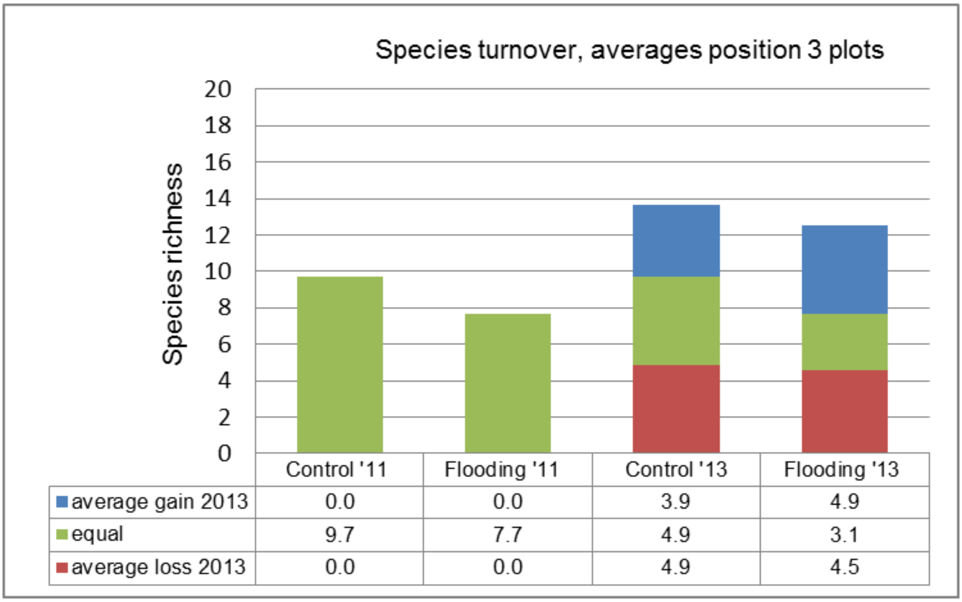
	Control '11	Flooding '11	Control '13	Flooding '13
🟦 average gain 2013	0.0	0.0	4.1	3.2
🟩 equal	9.0	6.2	4.6	2.7
🟥 average loss 2013	0.0	0.0	4.4	3.6



	Control '11	Flooding '11	Control '13	Flooding '13
🟦 average gain 2013	0.0	0.0	4.7	1.6
🟩 equal	8.1	4.9	4.3	2.1
🟥 average loss 2013	0.0	0.0	3.9	2.7



	Control '11	Flooding '11	Control '13	Flooding '13
🟦 average gain 2013	0.0	0.0	3.6	3.1
🟩 equal	9.0	6.2	4.7	2.8
🟥 average loss 2013	0.0	0.0	4.3	3.4



	Control '11	Flooding '11	Control '13	Flooding '13
🟦 average gain 2013	0.0	0.0	3.9	4.9
🟩 equal	9.7	7.7	4.9	3.1
🟥 average loss 2013	0.0	0.0	4.9	4.5

S5.3. Output Linear Mixed Models.

Dependent variable: Species richness

Type I Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	5,062	177,595	,000
temperature	1	5,062	4,092	,098
avN	1	58,741	8,255	,006
avP	1	45,400	1,995	,165
Ngrw	1	24,173	2,660	,116
Pgrw	1	79,181	,037	,849
biomass	1	75,765	13,467	,000
groundwaterlevel	1	32,509	12,773	,001
section	1	5,711	3,032	,135
section * groundwaterlevel	1	79,718	3,597	,062

a. Dependent Variable: speciesrichness.

Estimates of Fixed Effects[a]

Parameter	Estimate	Std. Error	df	t	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Intercept	-6,823006	5,470590	8,419	-1,247	,246	-19,329812	5,683800
temperature	1,537749	,582756	9,059	2,639	,027	,220782	2,854717
avN	-,048860	,092270	79,961	-,530	,598	-,232485	,134764
avP	-,021737	,035718	55,040	-,609	,545	-,093315	,049842
Ngrw	,056149	,047144	28,337	1,191	,244	-,040368	,152667
Pgrw	-2,512342	5,710793	76,527	-,440	,661	-13,885106	8,860421
biomass	-,001944	,000789	76,469	-2,464	,016	-,003515	-,000373
groundwaterlevel	-,093050	,027785	76,609	-3,349	,001	-,148381	-,037718
[section=,00]	2,872603	1,235936	7,571	2,324	,050	-,005816	5,751021
[section=1,00]	0[b]	0	.	.	.	.	.
[section=,00] * groundwaterlevel	,088869	,046857	79,718	1,897	,062	-,004385	,182122
[section=1,00] * groundwaterl	0[b]	0	.	.	.	.	.

a. Dependent Variable: speciesrichness.

b. This parameter is set to zero because it is redundant.

section[a]

section	Mean	Std. Error	df	95% Confidence Interval	
				Lower Bound	Upper Bound
,00	8,698[b]	,816	5,928	6,695	10,701
1,00	6,495[b]	,799	5,469	4,494	8,497

Dependent variable: biomass

Type I Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	4,990	385,783	,000
temperature	1	4,990	72,580	,000
avN	1	54,354	,017	,896
avP	1	22,597	16,332	,001
Ngrw	1	10,410	,687	,426
Pgrw	1	80,668	,059	,809
groundwaterlevel	1	40,977	2,183	,147
section	1	6,629	,078	,789
section * groundwaterlevel	1	68,903	4,761	,033

a. Dependent Variable: biomass.

Estimates of Fixed Effects[a]

Parameter	Estimate	Std. Error	df	t	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Intercept	-2039,281647	460,098703	9,210	-4,432	,002	-3076,486039	-1002,077256
temperature	291,366642	45,661814	7,952	6,381	,000	185,960086	396,773198
avN	-25,551634	12,054009	66,727	-2,120	,038	-49,613346	-1,489922
avP	13,491671	3,939858	21,797	3,424	,002	5,316499	21,666844
Ngrw	3,640396	4,861802	10,992	,749	,470	-7,061361	14,342153
Pgrw	-323,789684	808,105403	80,286	-,401	,690	-1931,882777	1284,303409
groundwaterlevel	8,444362	3,490072	62,326	2,420	,018	1,468534	15,420190
[section=,00]	-107,321105	112,059621	11,313	-,958	,358	-353,133416	138,491205
[section=1,00]	0[b]	0	.	.	.	.	.
[section=,00] * groundwaterlevel	-13,380835	6,132181	68,903	-2,182	,033	-25,614510	-1,147161
[section=1,00] * groundwaterlevel	0[b]	0	.	.	.	.	.

a. Dependent Variable: biomass.

b. This parameter is set to zero because it is redundant.

Section[a]

section	Mean	Std. Error	df	95% Confidence Interval	
				Lower Bound	Upper Bound
,00	800,418[b]	67,919	7,194	640,690	960,146
1,00	806,839[b]	64,148	6,004	649,903	963,775

Dependent variable: extractable soil N

Type I Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	5,822	8,992	,025
temperature	1	5,822	1,464	,273
avP	1	49,653	15,490	,000
Ngrw	1	24,275	,031	,861
Pgrw	1	80,475	,304	,583
biomass	1	77,109	3,308	,073
groundwaterlevel	1	29,465	3,799	,061
section	1	6,544	,619	,459
section * groundwaterlevel	1	80,899	1,505	,223

Dependent Variable: avN.

Estimates of Fixed Effects[a]

Parameter	Estimate	Std. Error	df	t	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Intercept	3,955660	6,387057	9,833	,619	,550	-10,308362	18,219683
temperature	-,165066	,682552	10,665	-,242	,813	-1,673130	1,342997
avP	,146011	,039511	52,385	3,695	,001	,066741	,225281
Ngrw	,016232	,055965	29,525	,290	,774	-,098142	,130605
Pgrw	-3,957700	6,876292	77,783	-,576	,567	-17,647948	9,732548
biomass	-,002029	,000925	78,162	-2,194	,031	-,003870	-,000188
groundwaterlevel	,064282	,032608	75,508	1,971	,052	-,000671	,129234
[section=,00]	-1,706489	1,431371	8,667	-1,192	,265	-4,963566	1,550588
[section=1,00]	0[b]	0	.	.	.	.	.
[section=,00] * groundwaterlevel	-,068610	,055928	80,899	-1,227	,223	-,179891	,042672
[section=1,00] * groundwaterlevel	0[b]	0	.	.	.	.	.

a. Dependent Variable: avN.

b. This parameter is set to zero because it is redundant.

section[a]

section	Mean	Std. Error	df	95% Confidence Interval	
				Lower Bound	Upper Bound
,00	1,138[b]	,945	6,794	-1,111	3,387
1,00	2,327[b]	,927	6,298	,086	4,569

Dependent variable: extractable soil P

Type I Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	6,645	24,067	,002
temperature	1	6,645	,057	,818
avN	1	31,617	14,719	,001
Ngrw	1	54,904	1,104	,298
Pgrw	1	68,440	2,069	,155
biomass	1	76,146	9,932	,002
groundwaterlevel	1	18,013	6,661	,019
section	1	6,917	,143	,716
section * groundwaterlevel	1	76,407	,047	,828

a. Dependent Variable: avP.

Estimates of Fixed Effects[a]

Parameter	Estimate	Std. Error	df	t	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Intercept	32,567661	27,360502	7,708	1,190	,269	-30,944906	96,080228
Temperature	-2,524334	2,887853	8,017	-,874	,407	-9,181279	4,132612
avN	,877342	,247587	77,499	3,544	,001	,384384	1,370300
Ngrw	,156729	,157461	75,982	,995	,323	-,156882	,470341
Pgrw	17,898714	16,058371	74,908	1,115	,269	-14,091843	49,889270
Biomass	,004780	,002167	76,347	2,205	,030	,000464	,009096
groundwaterlevel	,250080	,077559	76,820	3,224	,002	,095635	,404525
[section=,00]	2,651404	6,380557	7,538	,416	,689	-12,220607	17,523414
[section=1,00]	0[b]	0	.	.	.	.	.
[section=,00] * groundwaterlevel	,029237	,134327	76,407	,218	,828	-,238276	,296750
[section=1,00] * groundwaterlevel	0[b]	0	.	.	.	.	.

a. Dependent Variable: avP.

b. This parameter is set to zero because it is redundant.

section[a]

section	Mean	Std. Error	df	95% Confidence Interval	
				Lower Bound	Upper Bound
,00	16,441[b]	4,421	6,968	5,978	26,904
1,00	14,010[b]	4,395	6,811	3,559	24,462

Dependent variable: species richness of seeds

Type I Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	2,854	73,827	,004
temperature	1	2,854	6,085	,095
biomass	1	17,346	,123	,730
groundwaterlevel	1	46,005	13,255	,001
section	1	3,457	,634	,477
section * groundwaterlevel	1	45,764	,503	,482

a. Dependent Variable: speciesseed.

Estimates of Fixed Effects[a]

Parameter	Estimate	Std. Error	df	t	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Intercept	-5,471275	4,603161	3,334	-1,189	,312	-19,323442	8,380891
temperature	1,336675	,490313	2,985	2,726	,073	-,228045	2,901394
biomass	-,001017	,001104	46,645	-,921	,362	-,003239	,001205
groundwaterlevel	,142500	,042593	47,777	3,346	,002	,056851	,228149
[section=,00]	,331224	1,537123	8,046	,215	,835	-3,209864	3,872312
[section=1,00]	0[b]	0	.	.	.	.	.
[section=,00] * groundwaterlevel	-,052294	,073764	45,764	-,709	,482	-,200793	,096205
[section=1,00] * groundwaterlevel	0[b]	0	.	.	.	.	.

a. Dependent Variable: speciesseed.

b. This parameter is set to zero because it is redundant.

section[a]

section	Mean	Std. Error	df	95% Confidence Interval	
				Lower Bound	Upper Bound
,00	5,342[b]	,900	3,897	2,817	7,867
1,00	4,547[b]	,854	3,154	1,903	7,191

a. Dependent Variable: speciesseed.

b. Covariates appearing in the model are evaluated at the following values: temperature = 8,9633, biomass = 686,2889, groundwaterlevel = -8,8738.

Dependent variable: number of seeds

Type I Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	48	26,693	,000
temperature	1	48	5,129	,028
biomass	1	48	,049	,825
groundwaterlevel	1	48	2,541	,118
section	1	48	,011	,918
section * groundwaterlevel	1	48	,061	,806

a. Dependent Variable: seednumber.

Estimates of Fixed Effects[a]

Parameter	Estimate	Std. Error	df	t	Sig.	95% Confidence Interval	
						Lower Bound	Upper Bound
Intercept	-98,378085	90,525527	48	-1,087	,283	-280,391856	83,635685
temperature	21,152734	9,272466	48	2,281	,027	2,509191	39,796277
biomass	-,027787	,032886	48	-,845	,402	-,093909	,038334
groundwaterlevel	1,640450	1,244615	48	1,318	,194	-,862017	4,142917
[section=,00]	-9,381329	37,033285	48	-,253	,801	-83,841739	65,079081
[section=1,00]	0[b]	0	.	.	.	.	.
[section=,00] * groundwaterlevel	-,548576	2,217920	48	-,247	,806	-5,008003	3,910851
[section=1,00] * groundwaterlevel	0[b]	0	.	.	.	.	.

a. Dependent Variable: seednumber.

b. This parameter is set to zero because it is redundant.

section[a]

section	Mean	Std. Error	df	95% Confidence Interval	
				Lower Bound	Upper Bound
,00	53,080[b]	18,616	48	15,650	90,511
1,00	57,594[b]	16,470	48	24,478	90,709

a. Dependent Variable: seednumber.

b. Covariates appearing in the model are evaluated at the following values: temperature = 8,9633, biomass = 686,2889, groundwaterlevel = -8,8738.

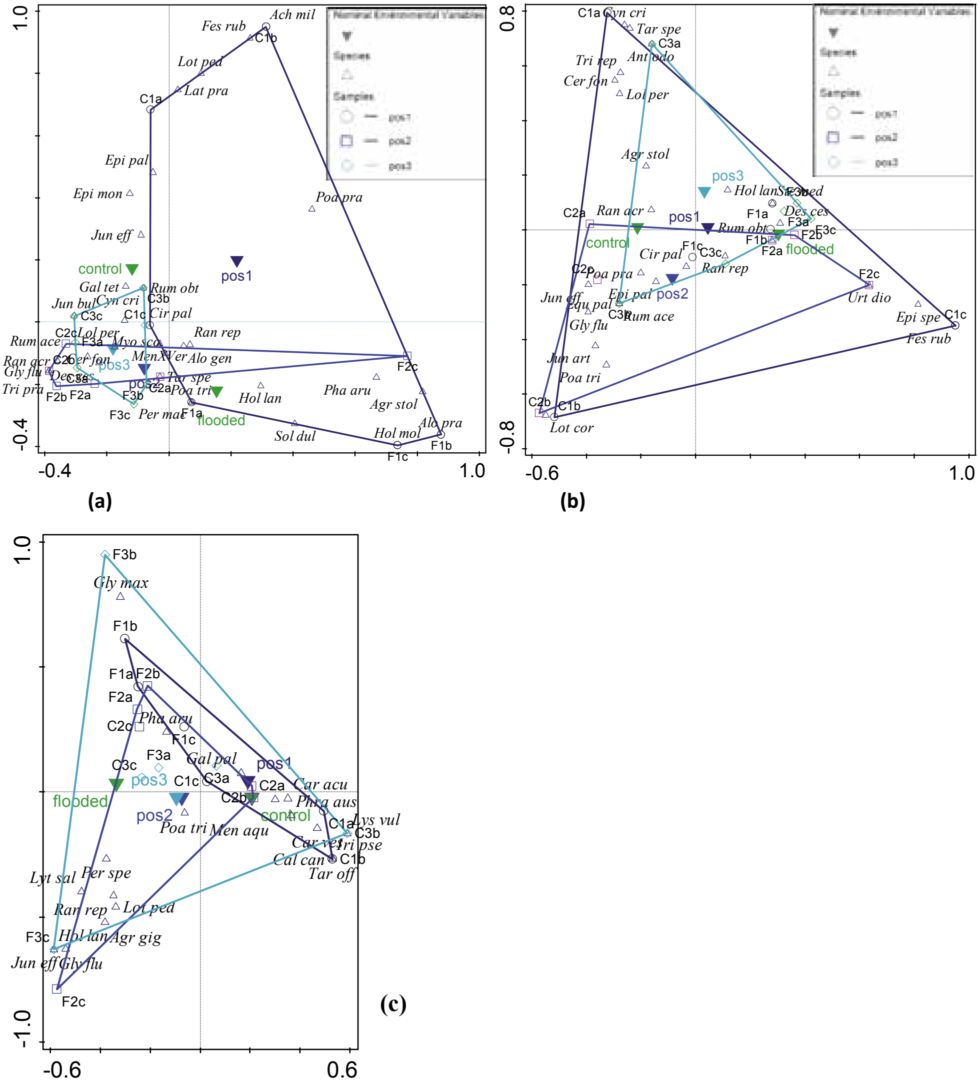
S5.4. Statistics supporting the CA in Fig. 5.4: Correlations between the case scores and supplementary variables, derived from response variable positions. These correlations are weighted in unimodal methods.

Variable	**Correlations axis 1**	**Correlations axis 2**
Latitude	0.9077	0.0615
Temperature	−0.8753	−0.1190
Surface water P	−0.7848	−0.3223
Biomass	−0.6202	−0.1099
Surface water N	−0.5398	0.2134
Groundwater N	−0.4231	−0.3638
Groundwater P	0.3623	0.1295
Water level	−0.3035	0.3659
Extractable soil N	0.3030	−0.0164
Rainfall	0.2612	0.2014
Extractable soil P	0.0693	−0.2940

S5.5. Species list of riparian vegetation found along the five investigated stream riparian gradients (at sampling plots of 50 x 50 cm) in 2013.

Voel baek	**Sandemands-baekken**	**Boye**	**Verloren beek Oosterhuizen**	**Groote Molenbeek**
Achillea millefolium *Agrostis stolonifera* *Alopecurus geniculatus* *Alopecurus pratensis* *Cerastium fontanum* *Cirsium palustre* *Cynosurus cristatus* *Deschampsia cespitosa* *Epilobium montanum* *Epilobium palustre* *Festuca rubra* *Galeopsis tetrahit* *Glyceria fluitans* *Holcus lanatus* *Holcus mollis* *Juncus bulbosus* *Juncus effusus* *Lathyrus pratensis* *Lolium perenne* *Lotus pedunculatus* *Mentha x verticillata* *Myosotis scorpioides* *Persicaria maculosa* *Phalaris arundinacea* *Poa pratensis* *Poa trivialis* *Ranunculus acris* *Ranunculus repens* *Rumex acetosa* *Rumex obtusifolius* *Solanum dulcamara* *Taraxacum species* *Trifolium pretense* --- 33 species	*Agrostis stolonifera* *Anthoxanthum odoratum* *Cirsium palustre* *Cynosurus cristatus* *Deschampsia cespitosa* *Epilobium palustre* *Festuca rubra* *Glyceria fluitans* *Holcus lanatus* *Poa pratensis* *Poa trivialis* *Rubus corylifolius* *Rumex acetosa* *Rumex obtusifolius* *Trifolium repens* *Stellaria media* *Juncus articulatus* *Juncus bufonius* *Juncus effusus* *Ranunculus repens* *Taraxacum species* *Lolium perenne* *Epilobium species* *Lotus corniculatus* *Equisetum palustre* *Ranunculus acris* *Urtica dioica* *Cerastium fontanum* --- 28 species	*Agrostis capillaris* *Agrostis gigantea* *Agrostis species* *Ajuga reptans* *Alopecurus geniculatus* *Alopecurus pratensis* *Calamagrostis canescens* *Carex hirta* *Carex remota* *Carex vulpina* *Cirsium palustre* *Dactylis glomerata* *Epilobium hirsutum* *Epilobium parviflorum* *Epilobium species* *Equisetum arvense* *Equisetum palustre* *Festuca rubra* *Filipendula ulmaria* *Geranium species* *Glechoma hederacea* *Holcus lanatus* *Juncus conglomeratus* *Juncus effusus* *Lathyrus pratensis* *Lotus pedunculatus* *Luzula campestris* *Lysimachia vulgaris* *Lythrum salicaria* *Mentha aquatica* *Myosotis scorpioides* *Phalaris arundinacea* *Phragmites australis* *Poa trivialis* *Rosa species* *Rubus fruticosus* *Scirpus sylvaticus* *Scrophularia nodosa* *Stellaria media* *Tussilago farfara* *Typha latifolia* *Valeriana officinalis* --- 42 species	*Agrostis gigantea* *Alnus glutinosa* *Galium palustre* *Glyceria maxima* *Holcus lanatus* *Poa trivialis* *Rubus corylifolius* *Rumex species* *Rumex acetosa* *Trifolium repens* *Taraxacum officinale* *Juncus effusus* *Veronica beccabunga* *Lotus corniculatus* *Equisetum palustre* *Equisetum fluviatile* *Hypochoeris radicata* *Juncus acutiflorus* *Lysimachia nummularia* *Scirpus sylvaticus* *Aegopodium podagraria* *Bidens species* *Equisetum arvense* *Lemna minor* *Plantago lanceolata* *Polygonaceae spec.* *Silene dioica* *Stachys palustris* --- 28 species	*Aegopodium podagraria* *Agrostis gigantea* *Alopecurus geniculatus* *Calamagrostis canescens* *Calystegia sepium* *Cardamine pratensis* *Cardamine species* *Carex acuta* *Carex vesicaria* *Cirsium arvense* *Epilobium species* *Epilobium tetragonum* *Galium palustre* *Glyceria fluitans* *Glyceria maxima* *Holcus lanatus* *Holcus mollis* *Hypochoeris radicata* *Iris pseudacorus* *Juncus acutiflorus* *Juncus effusus* *Lotus pedunculatus* *Lycopus europaeus* *Lysimachia nummularia* *Lysimachia vulgaris* *Lythrum salicaria* *Mentha aquatica* *Persicaria species* *Phalaris arundinacea* *Phragmites australis* *Poa trivialis* *Ranunculus repens* *Stachys palustris* *Stellaria media* *Taraxacum officinale* *Urtica dioica* --- 36 species

S5.6. Correspondence Analysis of vegetation composition along the stream riparian gradients. Plant species composition at the Voel Baek (a), Sandemandsbaekken (b), and Groote Molenbeek (c), 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 control versus flooding section. Position extremes are demarcated by envelopes (dark blue: pos. 1, mid blue: pos. 2, light blue: pos. 3).



Chapter 6

Structural and functional responses of plant communities to climate change-mediated alterations in the hydrology of riparian areas in temperate Europe

Annette Baattrup-Pedersen, Annemarie G. Garssen, Emma Göthe, Carl C. Hoffmann, Andrea Oddershede, Tenna Riis, Peter M. van Bodegom, Søren E. Larsen and Merel B. Soons

Ecology and Evolution (2018), 8, 4120–4135
doi: 10.1002/ece3.3973

Abstract

The hydrology of riparian areas changes rapidly these years because of climate change-mediated alterations in precipitation patterns. In this study, we used a large-scale in situ experimental approach to explore effects of drought and flooding on plant taxonomic diversity and functional trait composition in riparian areas in temperate Europe. We found significant effects of flooding and drought in all study areas, the effects being most pronounced under flooded conditions. In near-stream areas, taxonomic diversity initially declined in response to both drought and flooding (although not significantly so in all years) and remained stable under drought conditions, whereas the decline continued under flooded conditions. For most traits, we found clear indications that the functional diversity also declined under flooded conditions, particularly in near-stream areas, indicating that fewer strategies succeeded under flooded conditions. Consistent changes in community mean trait values were also identified, but fewer than expected. This can have several, not mutually exclusive, explanations. First, different adaptive strategies may coexist in a community. Second, intraspecific variability was not considered for any of the traits. For example, many species can elongate shoots and petioles that enable them to survive shallow, prolonged flooding but such abilities will not be captured when applying mean trait values. Third, we only followed the communities for 3 years. Flooding excludes species intolerant of the altered hydrology, whereas the establishment of new species relies on time-dependent processes, for instance the dispersal and establishment of species within the areas. We expect that altered precipitation patterns will have profound consequences for riparian vegetation in temperate Europe. Riparian areas will experience loss of taxonomic and functional diversity and, over time, possibly also alterations in community trait responses that may have cascading effects on ecosystem functioning.

Introduction

In temperate regions, such as Northern and Central Europe, climate change-associated alterations in precipitation patterns, with higher than average precipitation and less snow accumulation during winter and lower than average precipitation during summer, likely mediate significant alterations in the hydrological characteristics of lowland streams. In winter and early spring, an increase in the frequency, magnitude, and duration of flow events will occur (Karlsson et al., 2015; van Roosmalen et al., 2009; Thodsen et al., 2014), whereas the frequency and duration of drought periods are expected to increase during summer (Andersen et al., 2006; Christensen & Christensen, 2007). Higher temperatures will likely intensify deficits in water budgets during summer through enhanced evaporation and evapotranspiration, both of which will intensify water stress (Douville et al., 2002). Furthermore, higher temperatures may extend the active growth period of plants as growth may start earlier in spring and continue for a longer time, thereby possibly exacerbating the effects of flooding and droughts on natural ecosystems (Zwicke et al., 2013).

Climate change effects on the structural and functional properties of riparian ecosystems remain to be more fully elucidated. Increasing awareness of the importance of wetlands for a number of ecosystem services such as flood protection, water purification, water availability via groundwater recharge, and biodiversity has spurred new studies into the functioning of wetlands in a changing climate (see Catford et al., 2013; Kominoski et al., 2013; Garssen et al., 2014; Garssen et al., 2015 for an overview). Most of the studies conducted so far investigate the effects of climate changes on riparian community composition with focus on the response of a single species or restricted species assemblages (Catford et al., 2013; Garssen et al., 2014, 2015). A recent extensive review of plant community responses showed that prolonged flooding and increased inundation depth of riparian areas trigger significant shifts in species composition that may lead to either increased or decreased riparian species richness, depending on the environmental characteristics of the areas (Garssen et al., 2015). In Garssen et al. (2015), species richness was observed to generally decline at flooded sites in nutrient-rich catchments and at sites previously exhibiting relatively stable hydrographs (for instance rain-fed lowland streams; see e.g., Beltman et al., 2007; Baattrup-Pedersen et al., 2013), whereas an increase in species richness was detected at flooded sites in dry areas (e.g., in deserts and semi-arid climate regions where many streams are intermittent; see e.g., Stromberg et al., 2009; Horner et al., 2012). In contrast, almost all studies of the effects of increased drought episodes on riparian plant community responses have shown a decline in species richness, particularly for herbaceous species (e.g., Stromberg et al., 2005; Westwood et al., 2006; reviewed in Garssen et al., 2014). A > 30-day drought period threatens the survival of many species and usually entails a strong reduction in riparian plant biomass, and a high drought intensity (i.e., a 3–4 cm water table decline per day) may impair riparian seedling survival, thereby producing relatively rapid changes in riparian species composition (Garssen et al., 2014).

The functional trait characteristics of plant species will likely determine whether the species are able to survive under changed environmental conditions (Cornwell & Ackerly, 2009; Jung et al., 2014). Hence, trait-based predictions of the response of riparian communities to climate change are valuable. In contrast to taxonomic approaches, trait-based methods enable generalizations (i.e., identification of common responses) to be made across regions (Catford et al., 2013; Diaz et al., 2004). A wide range of traits can be used to describe the responses of species to their environment, and different traits may capture different aspects of resource use, habitat requirements, and stress responses (e.g., Suding et al., 2006; Thuiller et al., 2010). Traits related to life form characteristics, growth forms, growth rates, photosynthetic pathways, leaf morphology, and chemistry have all been used to identify plant responses to environmental conditions as they affect species growth, survival, and reproductive output (de Bello & Mudrak, 2013; Violle et al., 2007; Westoby & Wright, 2006).

In this study, we explored the effects of an experimentally altered hydrology on the taxonomic and functional trait characteristics of the vegetation and deposited seeds in riparian areas. To increase the predictive potential, we used a large-scale experimental approach in which we manipulated water levels to disentangle the effects of specific environmental changes from co-occurring environmental characteristics that may otherwise blur the responses (see Ackerly, 2004; Douma et al., 2012; Wright et al., 2003). An additional strength of this approach was that the direct large-scale water level manipulations applied permits creation of groundwater–surface water interactions resembling those likely to occur in riparian areas under current and expected rates of climatic change. To identify cross-regional consistent patterns responses in the vegetation, the experimental sites were located in Denmark, Germany, and the Netherlands. In some parts of the sites, we experimentally increased flooding in the winter/spring and in other parts of the sites we increased droughts in summer.

We analyzed regenerative traits and vegetative traits that we expected would change under altered hydrological conditions (Fig. 6.1). The selection of traits was based on theoretical considerations: Hydrological alterations are likely to affect traits associated with the ability to increase the water uptake and/or conserve water as well as traits associated with the ability to survive conditions with water surplus (Douma et al., 2012; Hough-Snee et al., 2015). The vegetative traits included leaf traits (specific leaf area, size, and mass), root traits(rooting depth and porosity), and canopy (maximum height) that may show an adaptive response to cope with an altered hydrology. Under drought conditions, we expected that the abundance of species with extensive rooting depths and species with dense stems, small and thick leaves, and low specific leaf areas would increase in abundance. These traits can serve to maximize water uptake and at the same time reduce water loss as the rate of transpiration generally decreases with declining specific leaf area and leaf mass (Wright et al., 2005; Swenson & Enquist, 2007; Poorter & Markesteijn, 2008; Douma et al., 2012; Fig. 6.1). Under flooded conditions, we expected that the abundance of species with traits associated with the ability to lower the metabolic activity (the “quiescence strategy”) or avoid unfavorable conditions (the “escape strategy”; Bailey-Serres & Voesenek, 2008) would increase. Therefore, we anticipated that the abundance of tall species would increase as these have more easy access to atmospheric oxygen than short species. Additionally, we expected that species able to form porous roots or aerenchyma in adventitious roots to facilitate oxygen transport to the apical root zone (Armstrong et al., 1994) would increase in abundance, as these traits can be critically important to maintain the exchange of gas under flooded conditions (Bailey-Serres & Voesenek, 2008; Garssen et al., 2015). We also considered regenerative traits associated with the ability to disperse under drought and flooded conditions, respectively, including seed mass, volume, and buoyancy. Specifically, we expected that species with a high seed mass would decline in abundance with enhanced flooding concomitantly with an increase in species with a high seed buoyancy and volume, reflecting the adaptive value of producing low mass but high volume buoyant seeds that can disperse efficiently by water (Douma et al., 2012).

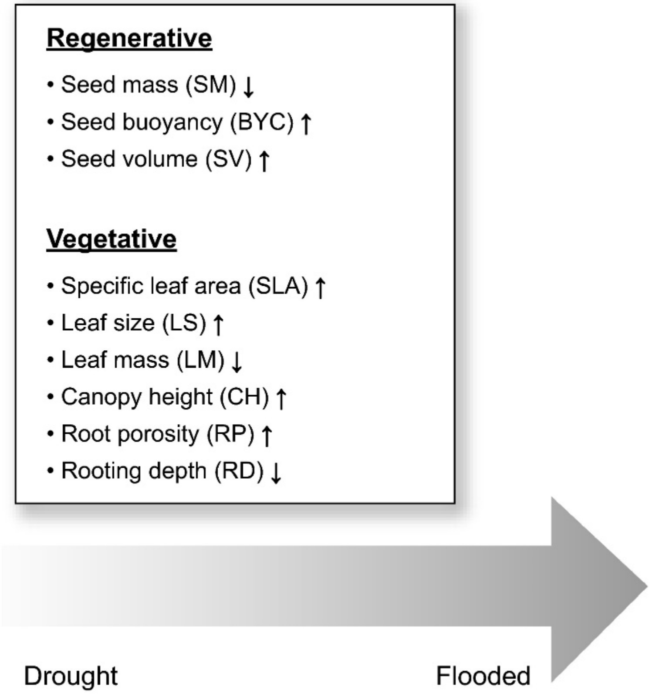


Fig. 6.1. Hypothesized changes in community trait composition moving from drought to flooded conditions. Arrows indicate whether a trait is expected to increase or decrease with increased flooding, with an expectation of the opposite response to drought.

The specific hypotheses tested were that flooding and drought mediate the following: (1) a decline in the taxonomic and functional diversity of traits and (2) a shift in the mean functional trait values as depicted in Figure 6.1. These responses will expectedly be strongest in near-stream areas where the hydrological alterations are most pronounced and will intensify over time. Additionally, it was tested if (3) the taxonomic diversity and functional diversity of the seed pool were higher in flooded areas than in drought areas as the regional species pool may contribute to diversity through species dispersal by water (i.e., hydrochory; Nilsson et al., 2010).

Materials and methods

Experimental setup

Four riparian areas situated along streams in Denmark (Sandemandsbækken 56.158507 N, 9.496120 E; Voel Bæk 56.195846 N, 9.703932 E), Germany (Boye 51°58′61.1″N, 6°91′10.01″E), and the Netherlands (Groote Molenbeek 51°39′17.32″N, 6°03′59.47″E) were selected for the experiment (Table 6.1). The four streams varied in mean discharge from 0.03 to 1.73 m^3/s. This was, however, not considered problematic as our sampling effort was focused on covering the natural features of the stream-riparian gradient at the study sites irrespective of size. That is, the sampling covered a gradient from the water table of the stream under summer base flow conditions to the high end of the floodplain where only extreme events lead to flooding (Fig. 6.2).

Table 6.1. Study site characteristics.

Site	Sandemands-bæk	Boye	Voel Bæk	Groote Molenbeek
Catchment area (km^2)	0.07	3.40	7.57	183.56
Grassland (%)	0.16	0.31	0.02	0.43
Forest (%)	0.43	0.11	0.03	0.00
Urban (%)	0.05	0.15	0.04	0.07
Agriculture (%)	0.25	0.42	0.90	0.45
Wetlands (%)	0.11	0.00	0.00	0.00
Water (%)	0.00	0.01	0.00	0.00
Mean discharge (m^3/s)	0.03	0.08	0.06	1.73

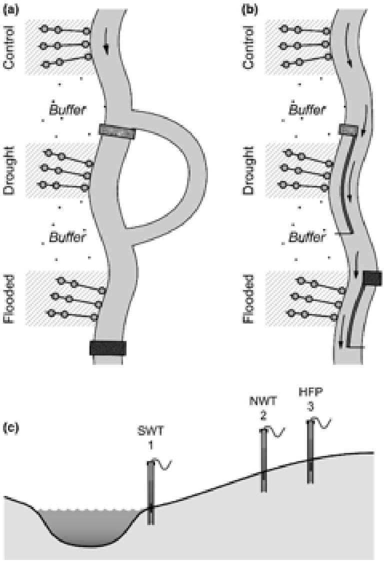


Fig. 6.2. A schematic presentation of the experimental setup applied in our study. The control section is situated upstream of the drought and flooded sections with buffers in-between. Flooding was created by constructing dams (marked as bars on the figure) to obstruct the water flow in the main channels. (a) In Denmark, a lateral dam of sandbags was constructed across the stream channel. (b) In Germany and the Netherlands, longitudinal dams were built within the channel, which together with a lateral dam across the channel obstructed the water flow in the main channel. (c) The position of the sample transects within the experimental sections. The first piezometer was placed just above the summer water table (position 1), the second piezometer just above the normal winter water table (position 2) and the third at the high end of the floodplain (position 3). The circles indicate the position of the piezometers along each transect.

The length of the experimental areas was 150 m, whereas width varied depending on the extent of the stream-riparian gradient. The areas were divided into three sections: a control section, a winter/ spring flooded section, and a summer drought section. These hydrological treatments were selected to mimic hydrological changes in Europe as predicted by IPCC (2007). The riparian areas had not been exposed to floodings prior to the experiment and comprised seminatural grassland communities with only herbaceous species.

The control sections were situated upstream of the manipulated sections with buffer areas in-between (Fig. 6.2). Flooding was created by constructing dams in the streams to obstruct the water flow in the main channels. In Denmark, a lateral dam made of sandbags was established across the stream channel (Fig. 6.2a), while in Germany and the Netherlands, longitudinal dams were built within the channel, which together with a lateral dam across the channel obstructed the water flow in the main channel (Fig. 6.2b). The constructed dams were used to create a 6-week flooding of the adjacent riparian areas (from March to mid-April) in 2011, 2012, and 2013, where the strongest responses were expected to occur in the final year of sampling given that the areas have been subject to manipulation for several years. However, in 2013, flooding was delayed in Denmark due to ice cover and lasted from the end of April to mid-June. In Denmark, summer droughts were created by digging a ditch, which together with a lateral dam in the main channel diverted part of the water flow from the main channel, resulting in a lowered water table within the experimental areas (Fig. 6.2a). In Germany and the Netherlands, a longitudinal dam was constructed across the stream channel, which together with a lateral dam across the channel obstructed the water flow adjacent to the experimental area, thereby lowering the water table (Fig. 6.2b). The drought experiment was conducted in 2011, 2012, and 2013 from the end of June to September (approximately 10 weeks) at all sites except Boye where strong groundwater seepage prevented reduction in the water table in the drought section.

Within each section, three sample transects were established perpendicular to the stream from the channel and upwards in the riparian areas (Fig. 6.2). The length of the sample transects varied among the study sites in order to represent a gradient from the lowest water table of the stream under summer base flow conditions to the highest point of the stream valley potentially flooded by surface water during extreme winter floods (Fig. 6.2c). To determine the hydrology of the control, drought, and flooded sections, a total of nine piezometers were installed within each section (three along each sample transect). The first piezometer was placed close to the stream, just above the normal summer water table in the stream, that is normally not flooded during summer but occasionally during winter floods (position 1; Fig. 6.2c). The second piezometer was placed at the highest point of the floodplain that was rarely flooded and, if so, only during extreme winter flooding events (once every 100 years; position 3; Fig. 6.2c).

Characterization of hydrology and vegetation

The water table depths were measured at least four times during the experimental periods in each experimental year (at the start of the experiment, after 2 weeks, after 4 weeks, and at the end of the experiment). Mean values of water table depths are given in Table 6.2. Positive values indicate that flooding occurred; the more positive the values, the higher the flooding depths. Similarly, negative values indicate that the water table is situated below the surface, and the more negative the values, the deeper the water table. Close to the streams (position 1), the flooding treatment prolonged the duration of winter flooding and increased the depth of flooding, whereas the drought treatment generally lowered the groundwater table during the treatment period (Table 6.2). Further away from the stream at position 2, the flooding treatment resulted in occasional winter floodings during the treatment period, whereas the drought treatment lowered the groundwater table (Table 6.2). Farthest away from the stream (position 3), the flooding treatment resulted in overall higher groundwater tables during the treatment period, whereas the drought treatment lowered the groundwater table (Table 6.2).

Vegetation surveys were conducted during the growing season (June–September). Percentage coverage was estimated for all vascular species in a total of 27 plots (50 × 50 cm^2) per site for each treatment. These were positioned with three plots next to each of the three piezometers in each of the three transects. Species composition was recorded according to the Braun-Blanquet method (1928), adjusted by Barkman, Doing, and Segal (1964). In the two Danish sites, an additional 27 bare plots were established with three plots next to each of the three piezometers in each of the three transects in order to follow the establishment of the vegetation under the new hydrological settings during the experimental period. These were created by removing the existing vegetation and the topsoil followed by deposition of 15 cm mixed sand and peat. To avoid ingrowth of nearby plants, the plots were delineated using 15-cm-wide plastic bands that were vertically inserted into the soil.

Vegetation data were converted to Ord% scale (coverage ranges from 0.5 to 140) according to Van der Maarel (2007) for a cover-based interpretation of the Braun-Blanquet scale (Braun-Blanquet, 1928). Seed traps consisting of 25 × 22.5 cm artificial mats with plastic bristles (Astroturf®) were placed and secured near the square plots used for vegetation surveys. Seeds were collected in 2011 in both control, flooded, and drought areas during the 6 weeks of experimental flooding and 10 weeks of experimental drought. The mats were removed from the field immediately after the experimental period and taken to the laboratory where they were stored in plastic bags in the dark at 4°C before processing. The processing involved extraction of deposited material by flushing the seed traps with water, followed by wet sieving the deposits to remove fine silt and clay. The material was then dried at 70°C for 48 hr after which intact seeds were visually identified from the dried material, manually removed, and

Table 6.2. Means and *SE* of groundwater table depths measured in piezometers at least four times during each experimental run (at the start of the experiment, after 2 weeks, after 4 weeks, and at the end of the experiment). Positive values indicate that the water table was situated above the ground surface, and negative values indicate that the water table was situated below the ground surface. The piezometers were placed along a hydrological gradient. The first sampling point was at the lowest water table of the stream during summer base flow conditions (SWT). The second sampling point was just above the normal winter water table that is normally not flooded in either summer or winter (position 2). The third sampling point was at the highest point up the stream valley that could be flooded by surface water during extreme winter floods (position 3).

Site	Treatment	Position	Groundwater, mean (cm)	Groundwater, SE
Sandemandsbæk	Control	1	-10.35	1.68
		2	-22.35	1.73
		3	-16.59	1.32
	Drought	1	-18.86	1.44
		2	-26.75	1.89
		3	-20.93	2.45
	Flooded	1	1.34	1.90
		2	-0.77	2.27
		3	-26.43	1.07
Voel	Control	1	-10.07	0.94
		2	-16.13	1.01
		3	-29.36	1.56
	Drought	1	-35.23	1.73
		2	-49.35	2.20
		3	-56.10	2.39
	Flooded	1	1.10	1.79
		2	-0.50	1.77
		3	-24.28	1.63
Boye	Control	1	-8.79	1.81
		2	-9.96	2.13
		3	-22.74	3.36
	Flooded	1	13.70	2.10
		2	-0.18	3.68
		3	-30.12	2.12
Groote Molenbeek	Control	1	-5.27	3.09
		2	-15.87	2.53
		3	-21.52	3.48
	Drought	1	-8.72	1.78
		2	-33.00	2.14
		3	-37.75	3.14
	Flooded	1	13.55	4.62
		2	1.29	2.89
		3	-4.50	1.39

determined to species level with the use of the "Digital seed atlas of the Netherlands" (Cappers et al., 2006).

Diversity indices and community-weighted means of plant traits

All diversity and trait indices were calculated for each vegetation type based on Ord% values (van der Maarel 2007). We calculated taxon richness and Shannon diversity as indices of taxonomic diversity. Traits were allocated to the encountered species based on information available in the LEDA database (Kleyer & Bekker, 2008) and literature cited in Douma et al. (2012). We selected traits describing both seed (SM, BYC, SV; Table 3) and adult (SLA, LS, LM, CH, RP, RD; Table 3) plant characteristics expected to respond to an altered hydrological regime as described in the introduction (Fig. 6.1). The number of species with trait information and the total abundances of these species are given in Table 6.3. We calculated functional divergence (FDvar) and community-weighted means (CWMs) when the abundance of species with trait information was above 65%, thereby precluding specific leaf area, root porosity, and rooting depth (Table 6.3). The abundance limit represented a balance between on the one hand to have as many traits as possible integrated in the analyses to obtain insight into the functional response of the plant community to climate change-related alterations in the hydrology of the areas, and on the other hand to keep the estimation bias low (Borgy et al., 2017). FDvar and CWMs were calculated for each trait according to Lavorel et al. (2007).

Table 6.3. Explanations of the traits used to characterize the riparian plant communities. Traits were derived from the LEDA database (Kleyer & Bekker, 2008) and from literature cited in Douma et al. (2012). The percentage of species with trait information was calculated as the number of species with trait information and as the abundance of species with trait information (in brackets). Three traits were excluded from the analyses (SLA, RD, RP) as the abundance of species with trait information was below 65%.

Trait name	Unit	Category	% species with trait information
Seed buoyancy (BYC)	%	Seed	64 (65)
Seed mass (SM)	Mg	Seed	75 (78)
Seed volume (SV)	mm^3	Seed	68 (73)
Specific leaf area (SLA)	mm^2/ mg	Adult	52 (55)
Leaf size (LS)	mm^2	Adult	64 (70)
Leaf mass (LM)	Mg	Adult	62 (68)
Canopy height (CH)	M	Adult	74 (77)
Root porosity (RP)	%	Adult	31 (53)
Rooting depth (RD)	M	Adult	37 (65)

A response ratio (Δr) (Osenberg et al., 1997) for each diversity and trait metric was also calculated using mean values of three sample plots for each of the three sampling transects for each position as:

$$\Delta r = ln\left(\frac{Nt}{Nc}\right)$$

where Nc is the mean metric value at the control site and Nt is the metric value for the treatment (flooded or drought). Response ratios allowed us to assess the general effects of the two treatments on riparian plant diversity and trait composition across the four streams.

Data analyses

All analyses described in this paragraph were conducted using the statistical software R (R Core Team 2014), package vegan (Oksanen et al., 2014). Canonical correspondence analysis (CCA) (function cca) followed by permutational ANOVAs (function anova.cca with maximum permutations set to 9999) was performed to assess differences in plant community composition between treatments (control, drought, flooding), type of vegetation (seed, existing vegetation, bareplot), and year (2011, 2012, 2013). To estimate the unique effect of a single predictor (i.e., treatment, type of vegetation, and year), the variation in plant community composition explained by the other predictors was always partialled out (i.e., included as covariables) in the ANOVAs. We also assessed which traits were significantly associated with differences in plant community composition between treatments by fitting trait vectors (describing the relative abundance of traits in each plot; i.e., CWMs) onto the CCA ordination using the function envfit. The envfit function finds the direction in the ordination space toward which each trait vector changes most rapidly and to which it is maximally correlated with the ordination configuration. The significance of the trait vectors was determined by a permutation test (n = 999).

To assess the general effects of the treatments across the study streams, we combined the yearly estimates into a single effect size measurement and tested whether the response ratios (Δr) of taxonomic diversity, trait diversity, and CWMs differed significantly from zero (i.e., higher or lower than zero) using two- sided t tests. The yearly response ratio estimates were combined by a weighted average using the variance for year as the weight. T tests were performed separately for each vegetation type (seed, existing vegetation, bareplot). A significant result was interpreted as a consistent and detectable change in the metric value in the control site versus the treated (flooded or dry) site across the investigated streams.

Results

There were large variations in species composition among the four study sites regarding both type considered (i.e., seed pool, bare plot, and existing vegetation), treatment applied (i.e., control, drought, and flooding), and time of sampling (i.e., 2011, 2012 and 2013; Fig. 6.3 and 6.4; Table 6.4). The effects of the applied treatment on the compositional patterns in the experimental areas were significant for both the seed pool and the existing vegetation (Fig. 6.3 and 6.4; Table 6.4). Several of the traits used to describe the functional characteristics of the vegetation were associated with the main gradients in taxonomic composition (Tables 6.5 and 6.6), suggesting that they captured important underlying mechanisms responsible for the observed compositional changes.

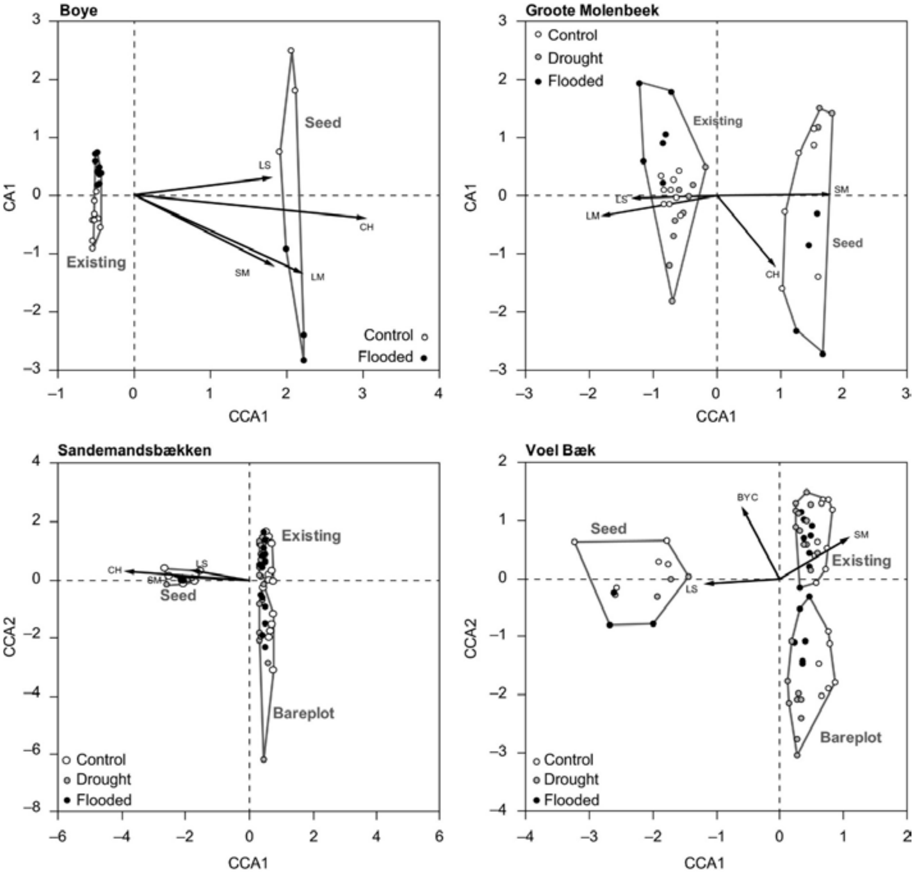


Fig. 6.3. Ordination plots of the canonical correspondence analyses (CCAs) of plant species composition within each riparian area (Boye, Groote Molenbeek, Sandemandsbækken, and Voel Bæk). In the CCAs, species composition was constrained by the type of vegetation (seed, existing, and bareplot), whereas the variation in species composition explained by treatment (flood, drought, control) and year (2011, 2012, 2013) was partialled out. Traits significantly associated with the CCA axes ($p < .05$) are plotted onto the ordination.

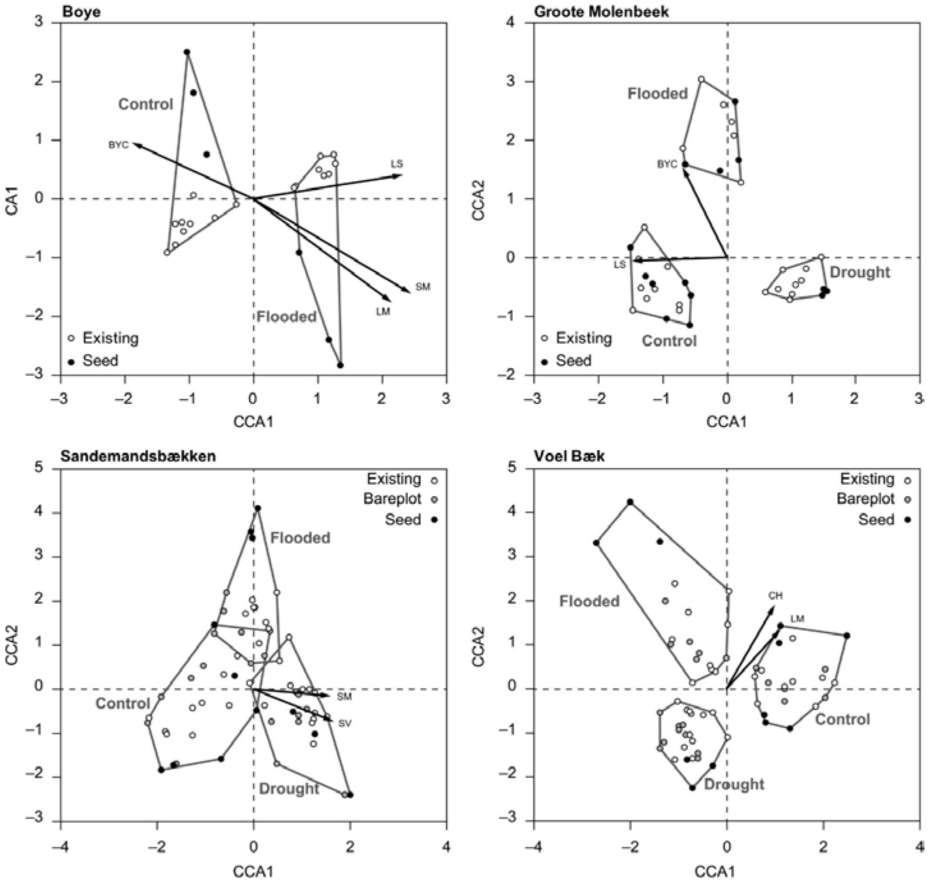


Fig. 6.4. Ordination plots of the canonical correspondence analyses (CCAs) of plant species composition within each stream (Boye, Groote Molenbeek, Sandemandsbækken, and Voel Bæk). In the CCAs, species composition was constrained by treatment (flood, drought, control), whereas the variation in species composition explained by type of vegetation (seed, existing, and bareplot) and year (2011, 2012, 2013) was partialled out. Trait vectors significantly associated with the CCA axes ($p < .05$) are plotted onto the ordination.

Table 6.4. Summary statistics of the ANOVAs of the canonical correspondence analyses where species composition was constrained by treatment, type, or year. The variation of the other parameters was always partialled out (i.e., included as covariables) in the ANOVAs to enable estimation of the unique effect of a single parameter.

Constraint	**Co-variables**	**Study site**	X^2	**F (Df)**	**Pr (>F)**
Treatment	Type; Year	Boye	0.352	2.571 (1.21)	0.005
		Groote Moolenbeek	0.537	2.847 (2.34)	0.005
		Voel	0.377	2.976 (2.58)	0.005
		Sandemand	0.432	2.682 (2.58)	0.005
Type	Treatment; Year	Boye	0.909	6.647 (1.21)	0.005
		Groote Moolenbeek	0.642	6.798 (1.34)	0.005
		Voel	0.680	5.409 (2.58)	0.005
		Sandemand	0.842	5.221 (2.58)	0.005
Year	Treatment; Type	Boye	0.352	1.224 (2.20)	0.079
		Groote Moolenbeek	0.409	2.084 (2.34)	0.005
		Voel	0.224	1.696 (2.58)	0.005
		Sandemand	0.269	1.614 (2.58)	0.005

Table 6.5. Summary statistics of the envfit analyses where trait vectors (CWMs) were fitted to the ordination axes of the canonical correspondence analyses (CCAs). Summary statistics of the correlation between trait vectors and the first two ordination axes are shown. In the CCAs, plant species composition was constrained by the type of vegetation, while treatment and year were included as covariables (i.e., the variation in plant composition explained by treatment and year was partialled out).

Trait	**Boye**				**Groote Moolenbeek**				**Sandemands bækken**				**Voel Bæk**			
	CCA1	CA1	r^2		CCA1	CA1	r^2		CCA1	CCA2	r^2		CCA1	CCA2	r^2	
BYC	-0.07	1.00	.05		0.80	0.60	.06		-0.53	0.85	0.07		-0.44	0.90	.21	**
SM	0.78	0.63	.30		-0.52	-0.85	.08		0.95	0.33	0.00		0.84	0.54	.18	**
SV	0.42	0.91	.10		-0.62	-0.79	.02		0.50	-0.87	0.02		0.54	0.84	.06	
LS	0.99	0.17	.32	**	-1.00	-0.03	.21	*	-0.99	0.12	0.12	*	-1.00	-0.07	.15	*
LM	0.85	-0.52	.63	**	-0.98	-0.19	.40	***	0.58	0.81	0.01		-0.89	-0.46	.07	
CH	0.99	-0.13	.88	***	0.60	-0.80	.26	**	-1.00	0.08	0.45	***	-0.68	0.73	.08	

***$p < .001$, **$p < .01$, *$p < .05$.

Table 6.6. Summary statistics of the envfit analyses where trait vectors (CWMs) were fitted to the ordination axes of the canonical correspondence analyses (CCAs). Summary statistics of the correlation between trait vectors and the first two ordination axes are shown. In the CCAs, plant species composition was constrained by treatment, while the type of vegetation and year were included as covariables (i.e., the variation in plant composition explained by treatment and year was partialled out).

Trait	**Boye**				**Groote Moolenbeek**				**Sandemands bækken**				**Voel Bæk**			
	CCA1	CA1	r^2		CCA1	CA1	r^2		CCA1	CCA2	r^2		CCA1	CCA2	r^2	
BYC	-0.89	0.46	0.25		-0.41	0.91	0.32		0.66	0.75	0.07		-0.02	1.00	0.07	
SM	-0.36	0.93	0.14		0.67	-0.75	0.02		1.00	-0.09	0.14	*	0.94	-0.35	0.01	
SV	0.53	0.85	0.11		-0.23	-0.97	0.02		0.91	-0.40	0.17	**	-0.70	-0.72	0.07	
LS	0.98	0.18	0.31	*	-1.00	-0.04	0.24	*	0.99	-0.11	0.03		-0.15	0.99	0.05	
LM	0.77	-0.63	0.43	**	-0.78	-0.63	0.15		-0.81	-0.59	0.04		0.64	0.77	0.11	*
CH	0.54	-0.84	0.02		-0.83	0.55	0.13		0.83	0.55	0.05		0.47	0.88	0.16	**

***$p < .001$, **$p < .01$, *$p < .05$.

Existing vegetation

Applying response ratios, we detected consistent changes among study sites for both the taxonomic and functional composition of the plant communities. In accordance with the first hypothesis, we observed that both species richness and Shannon diversity were negatively affected by drought and flooding and that the response varied with distance from the streams (Fig. 6.5). At position 1, the richness and diversity of the existing vegetation declined in response to drought the first year after initiating the treatment (i.e., the response ratio was significantly lower than zero), and richness was still lower after 3 years of treatment (Fig. 6.5.). Further away from the streams at position 2, we observed a decline in species richness and diversity, but the response was only significant after 3 years of flooding (Fig. 6.5.).

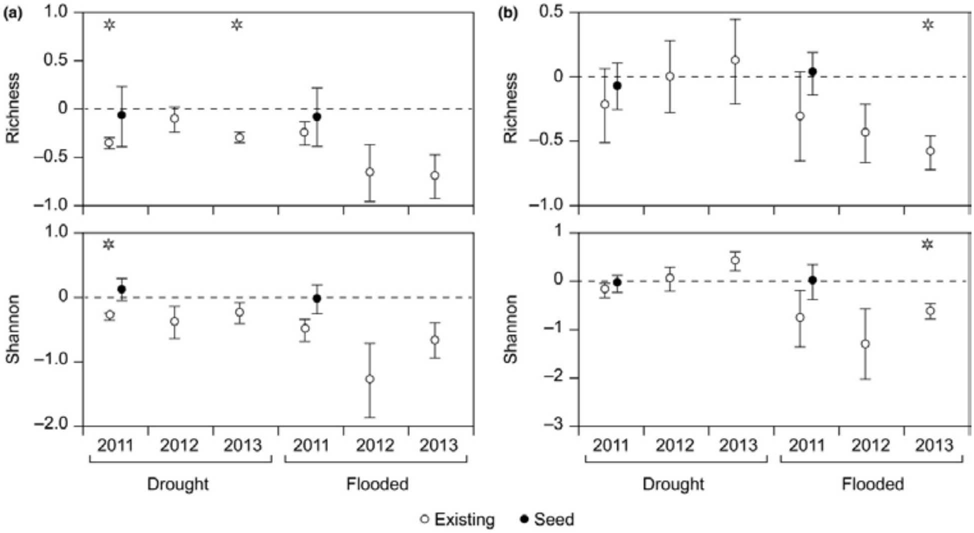


Fig. 6.5. Average response ratios (±1 *SE*) of taxonomic diversity (richness and Shannon diversity) in plots positioned close to the stream channel just above the normal summer water table (position 1; a) and in plots situated just above the normal winter water table (position 2; b). No significant changes in richness or diversity occurred further up the floodplain, position 3, following the applied drought and flooding treatment. Open symbols (existing) comprise data for the vegetation surveys, whereas closed symbols (seed) comprise data for the seed trap surveys. The color of the asterisk indicates the type of vegetation differing significantly from zero (i.e., black asterisk = seed, white asterisk = existing).

In accordance with the second hypothesis, we also identified consistent changes in the functional diversity of the existing vegetation in particular in response to flooding (Fig. 6.6a, 6.7a, and 6.8a). Close to the streams, at positions 1 and 2, we observed that the functional diversity of all traits declined in response to 3 years of flooding (BYC, SM, SV, CH, LM, and LS; Fig. 6.6a and 6.7a), whereas the functional diversity of CH declined in response to 3 years to drought but only at position 1 (closest to the stream). Farthest away from the streams at position 3, we observed a decline in the functional diversity of two traits (LM and LS) in response to drought (Fig. 6.8).

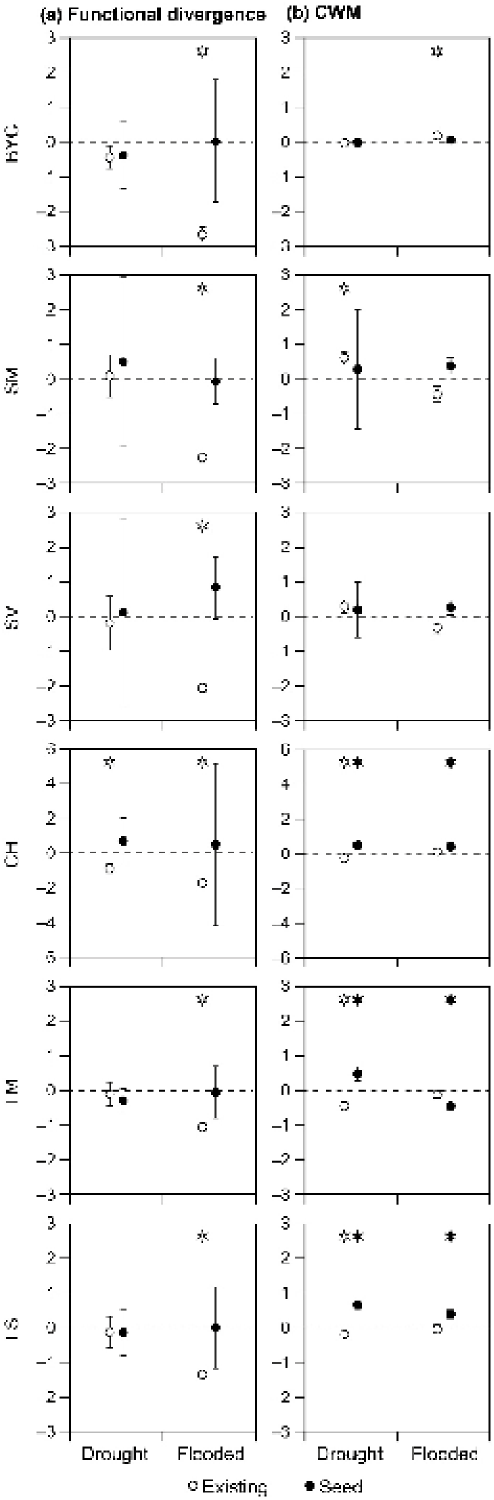


Fig. 6.6. Average response ratios (±1 *SE*) of functional trait diversity (FDis) (a) and trait composition (CWMs) (b) in plots positioned close to the stream channel just above the normal summer water table (position 1). When a response ratio is significantly different from zero, this is indicated with an asterisk above the error bar (p < .05). Open symbols (existing) comprise data for the vegetation surveys, whereas closed symbols (seed) comprise data for the seed trap surveys. The color of the asterisk indicates the type of vegetation differing significantly from zero (i.e., black asterisk = seed, white asterisk = existing). Note that the scale for FDis for CH is different in comparison with the other traits.

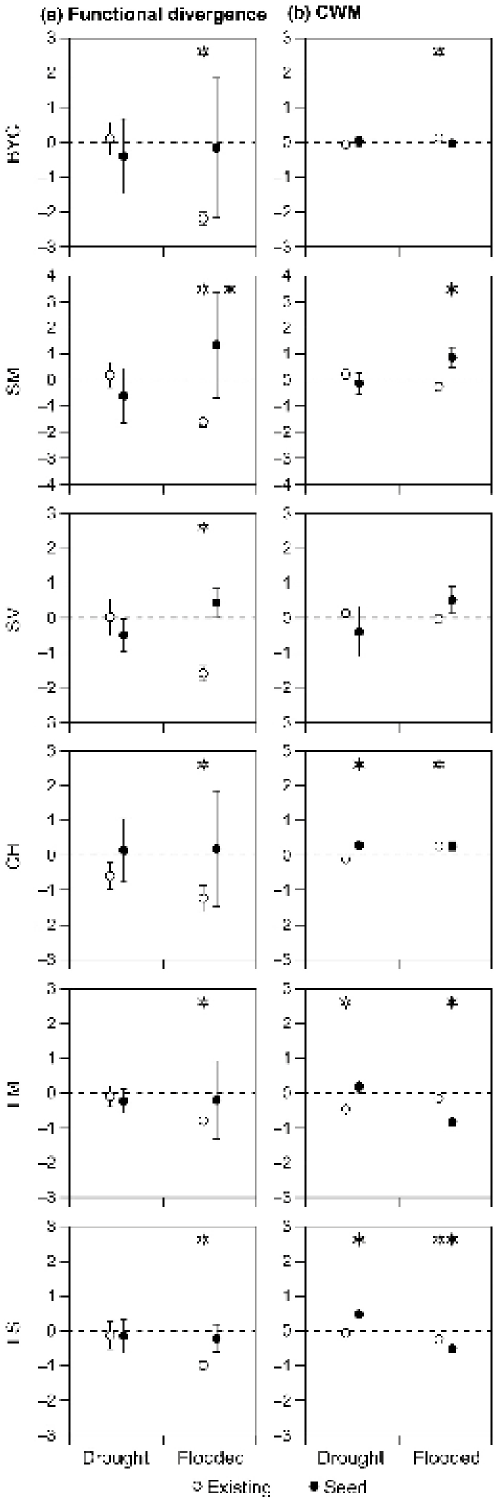


Fig. 6.7. Average response ratios (±1 *SE*) of functional trait diversity (FDis) (a) and trait composition (CWMs) (b) in plots positioned just above the normal winter water table (position 2). When a response ratio is significantly different from zero, this is indicated with an asterisk above the error bar (p < .05). Open symbols (existing) comprise data for the vegetation surveys, whereas closed symbols (seed) comprise data for the seed trap surveys. The color of the asterisk indicates the type of vegetation differing significantly from zero (i.e., black asterisk = seed, white asterisk = existing. Note that the scale for FDis for SM is different in comparison with the other traits.

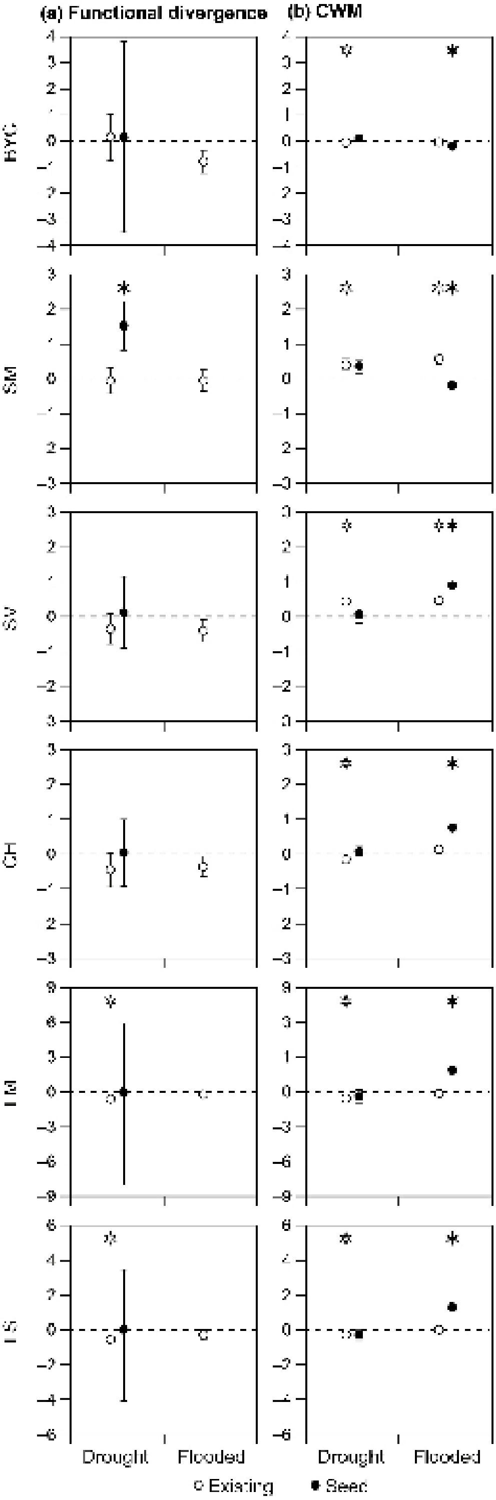


Fig. 6.8. Average response ratios (±1 *SE*) of functional trait diversity (FDis) (a) and trait composition (CWMs) (b) in plots positioned at the high end of the floodplain (position 3). When a response ratio is significantly different from zero, this is indicated with an asterisk above the error bar ($p < .05$). Open symbols (existing) comprise data for the vegetation surveys, whereas closed symbols (seed) comprise data for the seed trap surveys. The color of the asterisk indicates the type of vegetation differing significantly from zero (i.e., black asterisk = seed, white asterisk = existing). Note that the scale for FDis for BYC, LM, and LS is different in comparison with the other traits.

In accordance with the second hypothesis, we also observed consistent changes in the mean functional trait (CWM) values of the existing vegetation in response to the applied treatments and, as demonstrated by the diversity patterns, the response varied with distance from the streams (Fig. 6.6b, 6.7b, and 6.8b) and generally followed the predicted patterns (see Fig. 6.1). Close to the streams, at position 1, BYC-CWM increased in response to flooding and SM-CWM increased in response to drought (Fig. 6.6b) but, in contrast to our expectations, SV-CWM declined in response to flooding. Further away from the stream, at position 2, BYC-CWM and CH-CWM increased in response to flooding and LS-CWM declined (Fig. 6.7b), but in contrast to our expectations, LM-CMW declined in response to drought (Fig. 6.7b). Farthest away from the stream at position 3, we observed an increase in SV-CWM in response to flooding, also confirming our expectations (Fig. 6.8b), but SM-CWM increased which was in contrast to our expectations (Fig. 6.8b). We also observed several significant changes in the trait composition of the community in response to drought at position 3 (BYC, SM, CH, LS, SV, LM) and for the majority of the traits, these changes were as predicted (BYC, SM, CH, LS; Fig. 6.8b).

Seed pool

As opposed to our third hypothesis, we did not find a significant increase in the taxonomic richness or diversity of the seed pool in response to flooding (Fig. 6.5; ANOVA; $p > .05$), but we observed an increase in functional diversity but only for SM at position 2 (Fig. 6.7a). Instead, we observed several changes in the trait value of the seed pool in response to flooding (CH, LM, LS at position 1; SM, LM, LS at position 2; BYC, SM, SV, CH, LM, LS at position 3) and drought (CH, LM, LS at position 1; CH, LS at position 2) and most of these changes followed the predicted pattern (Fig. 6.1) particularly close to the stream.

Discussion

Taxonomic and functional diversity response

We found significant effects of flooding and drought on the species composition of both the vegetation and the seed pool in all study areas. Between-study site variability was also prominent, and this is likely due to local differences in soil characteristics and/or hydrological conditions among the study sites that influence the effects of hydrological alterations on the riparian vegetation (Garssen et al., 2015). Despite the observed between-study site variability, consistent patterns were also detected in response to hydrological changes. In particular, we observed a decline in both the taxonomic and functional diversity of the plant communities. The decline in taxonomic diversity in response to drought was only evident near the streams, probably reflecting that the experimental areas were already well drained and consequently less affected by the experiment (Table 6.2), whereas the negative impacts of flooding on species diversity were more pronounced (although only significant after 3 years of flooding). This finding may indicate that fewer species were able to tolerate flooding within the area compared with the number of species able to tolerate (relatively mild) drought and/ or that dispersal constraints were higher for species adapted to flooded conditions. Our findings are in line with those of Ström, Jansson, Nilsson, Johansson, and Xiong (2011) where soil monoliths were transplanted to areas subjected to different flooding intensities within the riparian zone of a boreal river. Species diversity increased rapidly in monoliths transplanted to higher elevations (i.e., less flooding) over the course of the 6-year field study, while species diversity in monoliths transplanted to lower elevations (i.e., more flooding) declined rapidly (Ström et al., 2011).

Functional diversity also responded to the altered hydrological settings, in particular in proximity to the streams. We observed a significant decline in the functional diversity of all traits, indicating that the range of successful strategies displayed under the new hydrological settings was restricted. Our finding lends support to previous studies suggesting that strong abiotic filters constrain the range of species mean trait values that can exist within the community, leading to a convergent trait distribution (Bernard-Verdier et al., 2012; Jung et al., 2010; Weiher et al., 1998). In line with our observations for taxonomic diversity, also functional diversity responded more strongly to flooding than drought, indicating that flooding poses a more severe stress on the riparian community in temperate regions (Fraaije et al., 2015b; Fraaije et al., 2015a). The loss of functional diversity (1–2 years) may influence resource use efficiency within the systems, with cascading effects on ecosystem functioning (Díaz & Cabido, 2001). Further studies are, however, needed to explore this topic, with special emphasis on how climate change-mediated alterations in hydrological extremes in combination with a higher degree of unpredictability in the occurrence of these affect ecosystem functioning.

Community functional trait response

The loss of functional diversity was also reflected in the mean trait response of the riparian plant community. We observed a consistent increase in the mean trait value of seed buoyancy in response to flooding, indicating that the fraction of species adapted to flooded conditions increased in the area. This finding is in accordance with Ozinga, Bekker, Schaminee, and Van Groenendael (2004) who, based on a classification of dispersal traits of ca. 900 species from different types of communities, found a highly significant correlation between the position of species along a wetness gradient and the frequency of morphological adaptations to hydrochory. This pattern has later been confirmed also for riparian and aquatic plant communities (van den Broek et al., 2005). As opposed to the findings of Douma et al. (2012), however, we did not observe a declining seed mass with enhanced buoyancy and seed density therefore seems to be a relatively poor predictor of seed buoyancy.

For the vegetative CWMs, we observed fewer consistent changes in comparison with those previously reported to respond to an altered hydrology (Bernard-Verdier et al., 2012; Jung et al., 2010; Mommer et al., 2005; Violle et al., 2011; Voesenek et al., 2006). There may be several, nonmutually exclusive, explanations to the less consistent response of trait CWMs to the contrasting hydrological settings in our study. First, different adaptive strategies for different species may co-occur in a community, which may partly explain the relatively weak response observed when comparing the mean trait value of single traits (Bernard-Verdier et al., 2012; Douma et al., 2012). For example, some species may have small and thin leaves that facilitate oxygen uptake during submergence (Banach et al., 2009; Nielsen & Sand-Jensen, 1989), enabling them to survive under flooded conditions, whereas other species may avoid flooded conditions by elongating their shoots, thereby accessing atmospheric oxygen (Voesenek et al., 2004) as also observed in our study. Second, intraspecific variability was not considered for any of the traits in this study, which may have weakened community responses (Albert et al., 2011; Jung et al., 2010). For example, many species can elongate shoots and petioles that enable them to survive shallow, prolonged flooding (e.g., Chen et al., 2009), but such abilities will not be captured when applying mean trait values. Third, we only followed the communities for 3 years after the change in hydrological settings. Altered hydrological conditions will likely mediate fast exclusion of species intolerant of these changes, whereas the establishment of new species relies on their dispersal and establishment within the areas. Therefore, a delay in the response of mean trait values of the community to changed habitat conditions may occur (Oddershede et al., 2015; Sandel et al., 2010), reflecting progressive filling of available niches within the community, eventually leading to stronger trait convergence (Helsen et al., 2012; Roscher et al., 2014). This delay may be stronger in existing vegetation than in bare plots where colonization and environmental filtering may occur rapidly (Fraaije et al., 2015b; Fraaije et al., 2015a) as also seen in the bare plots in our study, which differed significantly in species composition from the existing vegetation. Finally, we did not have traits for all species found in the areas, and the results regarding the response of community-weighted trait means should therefore be treated with caution.

Seeds

We expected to find functionally more diverse seed pools in the flooded areas than in the drought areas, reflecting that hydrochory can introduce seeds from an upstream species pool in addition to seeds that may enter from the local species pool by wind and/or animal dispersal. Furthermore, earlier investigations have shown that seed deposition in flooded areas is highly dependent on flow patterns and microtopography within the areas and that the amount of seeds deposited coincides with the drift line in flooded areas (Nilsson & Grelsson, 1990; Riis et al., 2014). We therefore expected to find the highest diversity at intermediate distance from the streams. However, our study did not confirm this expectation as the functional diversity was unaffected by flooding. This finding indicates that species arriving by water may not be more functionally diverse than those arriving by other means of dispersal. This interpretation is supported by previous studies reporting that species dispersed by hydrochory are often those already locally abundant (Brederveld et al., 2011; Soomers et al., 2011) and that flooding in itself may not be sufficient to increase species richness in grassland vegetation upon restoration of more natural flooding conditions (Baattrup-Pedersen et al., 2013b; Baattrup-Pedersen et al., 2013a; Bissels et al., 2004).

Conclusions

We observed large study site variability in plant community responses to the hydrological conditions of our experiment, regarding both drought and flooding. We did, however, identify consistent patterns in the taxonomic and functional responses of plant communities to the altered hydrological settings. Both taxonomic diversity and functional diversity were generally negatively affected by flooding and to some extent also by drought. These findings indicate that the range of successful strategies declined due to the altered hydrological settings. The loss in functional diversity was also reflected in the mean trait response of the riparian community but fewer significant and consistent changes appeared in response to the altered hydrological conditions. This might reflect a combination of the existence of several strategies within the vegetation to cope with the altered hydrological settings and a delay in the mean trait response due to a slow and progressive filling of available niches. Taken together, our results demonstrate that even though it is difficult within a 3-year time frame to predict general effects of extreme hydrological conditions on riparian vegetation characteristics across large regions, the observed losses in diversity likely affect ecosystem functioning by reducing niche complementarity with possible cascading effects on resource use efficiency.

Acknowledgments

This work was supported by the European Union 7th Framework Projects REFRESH under contract no. 244121 and MARS under contract no. 603378 (Annette Baattrup-Pedersen). We thank the landowners, water boards, and nature organizations for kindly allowing us to use their areas for our experiments, Marlene Venø Skjærbæk, Henrik Stenholt, Uffe Mensberg, and several students for hard work constructing the dams, Helena Kallestrup, Tinna Christensen and Juana Jacobsen for figure layout, Anne Mette Poulsen for editorial support and Frederik Hansen Baattrup for making the final editorial changes. The company AstroTurf® is acknowledged for sponsoring seed mats.

Chapter 7

Synthesis and perspectives for riparian wetland conservation

In 2018, large parts of Europe, including Atlantic Europe, experienced an exceptional dry spring and summer, resulting in low soil moisture conditions and large water deficits in stream and river water discharge (JRC, 2018). This constitutes a clear example of climate change, which is projected to increase temperatures, heat wave frequencies and extreme precipitation patterns. During such extreme drought episodes, streambeds dry up, plant biomass declines and plant mortality increases, since it is difficult or impossible for plants to extract water from the soil. This was in strong contrast to the summers of 2011 and 2012, which both had very wet periods in Atlantic Europe, and happened to be the first years of our experiments. In general, however, flooding episodes are expected to increase in winter or early spring. An example was the winter period in 2018, when large amounts of rainfall occurred and European stream and river discharges were high.

With this thesis I aimed at identifying the main effects of climate-driven increases in episodes of summer drought and winter flooding on the diversity and species composition of stream riparian plant communities and at systematically assessing the key factors involved. Our field experiments focused on stream riparian gradients in Atlantic Europe, making it possible to generate specific conclusions on the effects of flooding and drought episodes in this specific region of Europe and investigate the effects in the field. Many study results used in the meta-analyses were based on worldwide data and mesocosm experiments, mostly carried out in Northern hemisphere studies, which enabled a systematic investigation of universal effects of flooding and drought episodes on riparian vegetation. The meta-analyses and the results of the field experiments presented in this thesis showed many connections and enabled coherent interpretations. These combined results provide insights into relatively short-term responses of stream riparian vegetation under climate change. As shown in our meta-analyses as well as field studies, stream riparian plant communities respond quickly to increasing drought and flooding episodes, within a timespan of three years; individual plant responses take place within a period of approximately a month.

The meta-analysis on increased drought episodes included studies reporting on droughts that were more intense compared to our field experiment. Hence, results from the meta-analysis included stronger reponses of riparian plant species and communities to drought. Increased rooting depth, and reduced plant height and leaf area, leading to increased water use efficiency, were decisive for riparian plant survival as demonstrated in our meta-analysis. Both the meta-analysis and field results showed that a drought episode of 4–5 weeks can reduce riparian plant biomass rapidly and significantly. Our drought experiments demonstrated that in the top soil layer plant available nutrients, especially nitrogen, increased. The projected increase in duration and severity of drought episodes is sufficient to result in species shifts, and in case of extreme droughts leading to reduced riparian species richness and plant biomass. The meta-analysis evaluating the effects of increased flooding demonstrated that longer duration of flooding, greater depth of flooding and their combination reduced seedling survival of most riparian species. An increase in flooding depth also caused a decrease in riparian plant biomass. Several plant traits, such as the ability to elongate shoots and root porosity, were shown to be decisive for adult plant survival and growth during flooding. Both our meta-analysis and field experiment confirmed that the projected increase in duration and severity of flooding episodes is sufficient to result in rapid species shifts, leading to reduced species richness at sites in relatively nutrient-rich catchments. Our field experiments demonstrated that there was an overall decline in riparian species richness after 3 years of flooding, and riparian plant biomass increased. Extractable soil nitrogen and phosphorus increased, and there was a positive relation between extractable phosphorus and biomass, possibly affecting species richness. When comparing effects of our flooding and drought experiments in temperate Atlantic Europe on species richness and functional trait composition (Chapter 6), most pronounced effects occurred in the experiments with the enhanced flooding episodes. This is in agreement with the findings reported in the other chapters, which show negative effects of increased flooding on riparian plant diversity in nutrient-rich catchments and a relatively mild effect of increased drought in rain-fed catchments that still received considerable rainfall even while stream water tables were experimentally reduced.

The effects of increased drought and flooding episodes in temperate Atlantic streams on riparian plant communities can be briefly summarized as follows. More extreme drought and flooding conditions can rapidly lead to a decline in riparian species richness and an increase in the presence of species adjusted to drier or wetter conditions, respectively. Extreme drought episodes may narrow the riparian wetland zone with typical hydric species towards a strip at a relatively short distance to the streambed. An increased duration and intensity of flooding events may widen the zone with typical hydric species, but also reduce species richness due to increased nutrient availability and local mortality, caused by anaerobic conditions during flooding. This may lead to the replacement of rare species by more common species.

Due to their system-specific environmental gradients, riparian plant communities along lowland streams are in general characterised by high species richness, but many streams have been modified in the past. Their history of degradation and influence of human activities in general increase their vulnerable state (Tockner & Stanford, 2002; Naiman et al., 2005): riparian zones have been narrowed, excavated or removed entirely so there is little physical space for riparian species to persist or survive when conditions are temporally unfavourable. This is critical, because this severely limits the natural capacity of riparian wetlands to adapt to or mitigate climate change by their stabilizing properties (Capon et al., 2013; Collof et al., 2015) to retain their capacity to store water, remove nutrients and act as refuges for rare species. Nowadays, the negative impacts of human activities on riparian wetlands are increasingly being recognized and have led to river and stream restoration projects in the Netherlands such as ‘Valley wide stream restoration’ and the largescale project ‘Room for the river’, which aimed to restore the biodiversity, natural functioning and retention capacity of these riparian systems. However, results reported in this thesis suggest that even restored riparian plant communities in Atlantic and temperate Europe which are situated in nutrient-rich and already degraded, less resilient catchments with a past history of more stable hydrographs, are generally likely to be sensitive to extreme events.

Regional trends and perspectives for conservation

The results of the experiments and the meta-analyses enable us to present conservation options for stream riparian vegetation in the context of climate change. As explained above, riparian wetlands are often already vulnerable due to changes in catchment land use and are amongst the most degraded and impacted ecosystems in the world (Tockner & Stanford, 2002). Many stream riparian zones have been modified in the past (Verdonschot & Nijboer, 2002), which has resulted in a general decline of stream riparian species richness (Fraaije et al., 2006). All streams that were involved in the field experiments had been modified in the past, and were semi-natural streams with relatively high stream nutrient levels. Increased flooding episodes in these nutrient-rich catchments can negatively influence species richness, as demonstrated in our field experiments as well as in the literature (Baatrupp et al., 2013a; Beltman et al., 2007; Ström et al., 2011). Drought episodes can also substantially influence community composition and species richness, particularly in near-stream areas and with high drought intensity.

To mitigate the effects of these extreme flooding and drought episodes on stream riparian wetlands, it is critical that measures are taken at the relevant locations and the appropriate scales in the landscape to strengthen ecosystem resilience and enhance species richness. As the stream riparian wetland and its surroundings are historically connected hydrologically, biogeochemically and biologically, all these connections need to be considered on a landscape scale (REFRESH, 2014a; Verhoeven et al., 2008). This requires on the one hand preservation or restoration of wide, v-shaped riparian zones that allow for sufficient physical space along the hydrological gradient to secure and maintain riparian species diversity and ecosystem functions (Fraaije, 2016). On the other hand, preservation or restoration of riparian zones as riparian greenbelts along the entire corridors from headwaters to mouth are recommended (Tockner & Standford, 2002). Biodiversity declines associated with disrupted landscape connections generally weaken ecosystem functioning and stability (Isbell et al., 2015; Hautier et al., 2015; Tilman & Downing, 1994), resulting in less resilience to extreme episodes, thereby urging the need to consider and strengthen riparian species diversity and the connections between the stream, the riparian zone and the surrounding landscape.

In north-western Europe spatial developments regularly hamper the requirements needed for the restoration of natural and resilient, species-rich riparian zones (Verdonschot & Nijboer, 2015). For a robust restoration of degraded riparian zones, sufficient width and length for riparian zones is required, important for buffering properties and hydrological and biological processes, such as the storage and purification of water and requirements for species dispersal and provisioning of suitable habitat. Wide, natural gradients are prerequisites in riparian zones to be able to maintain species-rich stream riparian communities, since hydrological niches form the basis for species coexistence along hydrological gradients (Silvertown et al. 1999; Fraaije et al, 2015a & 2015b). A broad landscape approach is crucial to define which aspects need to be integrated for wetland restoration measures (Verhoeven et al., 2008). Wider and more diverse riparian wetlands provide habitat for more species and act as a reservoir of source populations to colonise newly available, disturbed sites (Brederveld et al., 2011; Soons et al., 2016). Conservation, and if necessary restoration is needed of wide, gradually sloping stream riparian wetlands bordering streams, with high internal heterogeneity (Fraaije et al, 2016). During extreme drought or flooding episodes, the refuges in heterogenic zones may allow the survival of source populations, and gradual slopes facilitate plant species movement upslope and downslope (REFRESH, 2014a).

Results from the meta-analysis as well as our field experiment focussing on increased flooding episodes, showed that negative effects of flooding on species richness in nutrient-rich catchments can rapidly take place. It is therefore crucial that water authorities and other involved partners focus on the reduction of stream, soil and groundwater nutrient loading in order to reach a good water quality for a robust riparian system. To achieve this, the EU Water Framework Directive is an important instrument, as it requires Member States to reach a good ecological status in rivers and streams (EEA, 2018). Also the objectives of the Habitats Directive, Natura 2000 and protection of natural ecosystem services in general, support mitigation of the negative effects of the projected increased drought and flooding episodes on riparian ecosystems through reduced nutrient loads. Thus, the predicted increased flooding episodes as a consequence of climate change require extra efforts in terms of riparian zone management, with a focus on 1) restoration of the hydrological buffering capacity of these riparian wetlands, by reserving sufficient space for the natural functioning of riparian wetlands, and 2) nutrient removal from surface waters and agricultural run-off, to preserve species-rich, resilient riparian areas.

According to literature, native plant communities vary widely in their vulnerability to climate change depending on the sensitivity of species to alterations of environmental variables and their ability to adapt to novel climatic conditions (Dawson et al., 2011). Apart from the predicted changes in species richness of native species, it is expected that more invasive non-native species will colonize and expand in riparian zones as a response to climate change. Altered riparian vegetation composition, including loss of native species and especially exotic invasions, are expected as a response to drought (Perry et al., 2012). In the meta-analysis focussing on the effects of drought, the response of species from the genus *Tamarix* was compared to *Populus* and *Salix* species (Garssen et al., 2014). *Tamarix* species thrive in a wide range of habitat conditions from flooded to dessicated, and also tolerate saline waters. Some of these *Tamarix* species are considered as invasive plants for their ability of rapid colonization and expansion (San-Miguel-Ayanz et al., 2016). Also other invasive species are expected to increase such as *Crassula helmsii*, an aquatic or riparian species, introduced by humans and currently invading more and more streams (as well as fens) in the Netherlands. Especially when disturbance in the ecosystem occurs, for instance after nature development or a dry period, *Crassula helmsii* can rapidly increase on bare sediments and become dominant (Van Kleef et al. 2017). Removal of invasive species and facilitation of native species by introduction during or directly following nature development, may increase the amount of competitors for nutrients and may stimulate ecosystem resilience by the increase in diversity.

In conclusion, recommendations for conservation and restoration include the design and implementation of critical measures that need to take place at the entire catchment scale, involving lateral and longitudinal connections along stream riparian wetlands. Restoration and preservation of wide, v-shaped stream valleys with a robust hydrological gradient across the riparian zone that maintains heterogeneity and connectivity, as well as the reduction of soil and water nutrient loads, are crucial to support resilient riparian ecosystems. These measures should be incorporated in management plans at the stream catchment scale, which are currently developed in the context of the EU Water Framework Directive. Next to conservation and restoration of riparian ecosystems with their characteristic biodiversity and ecosystem services, it is important to start systematic monitoring of the developments of biodiversity and ecosystem services in stream riparian ecosystems. This is important, since more extremes have occurred already (such as in 2018), which is an indication of what we can expect in the near future. Measuring the effects of these extreme events can help us to better estimate the long-term responses of stream riparian ecosystems to climate change.

References

Ackerly, D. (2004) Functional strategies of chaparral shrubs in relation to seasonal water deficit and disturbance. Ecological Monographs, 74, 25–44.

Albert, C.H., Grassein, F., Schurr, F.M., Vieilledent, G. & Violle, C. (2011) When and how should intraspecific variability be considered in trait- based plant ecology?. Perspectives in Plant Ecology, Evolution and Systematics, 13, 217–225.

Amlin, N.M. & Rood, S.B. (2002) Comparative tolerances of riparian willows and cottonwoods to water-table decline. Wetlands, 22, 338–346.

Andersen, H.E., Kronvang, B., Larsen, S.E., Hoffmann, C.C., Jensen, T.S., & Rasmussen, E.K. (2006) Climate- change mediated impacts on hydrology and nutrients in a Danish lowland river basin. Science of the Total Environment, 365, 223–237.

Armstrong, W., Brandle, R. & Jackson, M.B. (1994) Mechanisms of flood tolerance in plants. Acta Botanica Neerlandica, 43, 307–358.

Arnell, N.W. & Reynard, N.S. (1996) The effects of climate change due to global warming on river flows in Great Britain. Journal of Hydrology, 183, 397–424

Asamoah, S.A. & Bork, E.W. (2010) Drought tolerance thresholds in cattail (*Typha latifolia*): a test using controlled hydrologic treatments. Wetlands, 30, 99–110.

Auble, G.T., Friedman, J.M. & Scott, M.L. (1994) Relating riparian vegetation to present and future streamflows. Ecological Applications, 4, 544–554.

Auguie, B. (2017) gridExtra: Miscellaneous Functions for “Grid” Graphics. R package version 2.3.

Baattrup-Pedersen, A., Andersen, H.E., Larsen, S.E., Nygaard, B. & Ejrnæs, R. (2012) Predictive modelling of protected habitats in riparian areas from catchment characteristics. Ecological Indicators, 18, 227– 235.

Baattrup-Pedersen, A., Dalkvist, D., Dybkjær, J.B., Riis, T., Larsen, S.E. & Kronvang, B. (2013a) Species recruitment following flooding, sediment deposition and seed addition in restored riparian areas. Restoration Ecology, 21, 399–408.

Baattrup-Pedersen, A., Friberg, N., Larsen, S.E. & Riis, T. (2005) The influence of channelisation on riparian plant assemblages. Freshwater Biology, 50, 1248–1261.

Baattrup-Pedersen, A., Garssen, A.G., Göthe, E., Hoffmann, C.C., Oddershede, A., Riis, T., van Bodegom, P.M., Larsen, S.E. & Soons, M.B. (2018) Structural and functional responses of plant communities to climate change-mediated alterations in the hydrology of riparian areas in temperate Europe. Ecology and Evolution, 8, 4120–4135.

Baattrup-Pedersen, A., Jensen, K., Thodsen, H., Andersen, H.E., Andersen, P.M., Larsen, S.E., … Kronvang, B. (2013) Effects of stream flooding on the distribution and diversity of groundwater-dependent vegetation in riparian areas. Freshwater Biology, 58, 817– 827.

Baattrup-Pedersen, A., Riis, T., & Larsen, S.E. (2013b) Catchment characteristics and plant recruitment from sediment in stream and meadow habitats. River Research and Applications, 29, 855–863.

Bailey-Serres, J., & Voesenek, L.A.C.J. (2008) Flooding stress: Acclimation and genetic diversity. Annual Review of Plant Biology, 59, 313–339.

Banach, K., Banach, A.M., Lamers, L.P., De Kroon, H., Bennicelli, R.P., Smits, A.J. & Visser, E.J. (2009) Differences in flooding tolerance between species from two wetland habitats with contrasting hydrology: Implications for vegetation development in future floodwater retention areas. Annals of Botany, 103, 341–351.

Barkman, J., Doing, H. & Segal, S. (1964) Kritische Bemerkungen und Vorschläge zur quantitativen Vegetations-analyse. Acta Botanica Neerlandia, 13, 394–419.

Bates, B.C., Kundzewicz, Z.W., Wu, S. & Palutikof, J.P., Eds. (2008) Climate change and water. In: Technical Paper of the Intergovernmental Panel on Climate Change, pp. 210. IPCC Secretariat, Geneva.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67, 1-48.

Beltman, B., Willems, J.H. & Güsewell, S. (2007) Flood events overrule fertiliser effects on biomass production and species richness in riverine grasslands. Journal of Vegetation Science, 18, 625–634.

Bernard-Verdier, M., Navas, M.L., Vellend, M., Violle, C., Fayolle, A. & Garnier, E. (2012) Community assembly along a soil depth gradient: Contrasting patterns of plant trait convergence and divergence in a Mediterranean rangeland. Journal of Ecology, 100, 1422–1433.

Beumer, V., van Wirdum, G., Beltman, B., Griffioen J, Grootjans A.P. & and Verhoeven, J.T.A.M. (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.

Beumer, V., van Wirdum, G., Beltman, B., Griffioen, J. & Verhoeven, J.T.A. (2007) Biogeochemical consequences of winter flooding in brook valleys. Biogeochemistry, 86, 105–121.

Bissels, S., Holzel, N., Donath, T. W. & Otte, A. (2004) Evaluation of restoration success in alluvial grasslands under contrasting flooding regimes. Biological Conservation, 118, 641–650.

Bobbink, R., Hornung, M. & Roelofs, J.G.M. (1998) The effects of airborne nitrogen pollutants on species diversity in natural and seminatural European vegetation. Journal of Ecology, 86, 717–738.

Borenstein, M., Hedges, L.V., Higgins, J.P.T. & Rothstein, H.R. (2005) Introduction to Meta-Analysis. John Whiley & Sons Ltd, Chichester, U.K.

Borgy, B., Violle, C., Choler, P., Garnier, E., Kattge, J., Loranger, J., … Diquelou, S. (2017) Sensitivity of community- level trait–environment relationships to data representativeness: A test for functional biogeography. Global Ecology and Biogeography, 26, 729–739.

Braun-Blanquet, J. (1928). Pflanzensoziologie. Grundzüge der Vegetationskunde. In W. Schoenichen (Ed.), Biol. Studienbücher 7, pp. 1–330. Berlin, Germany: Springer.

Brederveld, R.J., Jaehnig, S.C., Lorenz, A.W., Brunzel, S. & Soons, M. B. (2011) Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. Journal of Applied Ecology, 48, 1241–1250.

Breheny, P. & Burchett, W. (2017) Visualization of Regression Models Using visreg. The R Journal, 9, 56-71.

Capon, S.J. (2005) Flood variability and spatial variation in plant community composition and structure on a large arid floodplain. Journal of Arid Environments, 60, 283– 302.

Capon, S.J., Chambers, L.E., Mac Nally, R., Naiman, B., Davies, P., Marshall, B., ... Williams, S.E. (2013) Riparian ecosystems in the 21st Century: Hotspots for climate change adaptation? Ecosystems, 16, 359–381.

Cappers, R.T.J., Bekker, R.M. & Jans, J.E.A. (2006) Digitale zadenatlas van Nederland (Digital Seed Atlas of the Netherlands). Groningen, The Netherlands: Barkhuis Publishing. www.zadenatlas.nl

Catford J.A. & Jansson R. (2014) Drowned, buried and carried away: effects of plant traits on the distribution of native and alien species in riparian ecosystems. New Phytologist, 204, 19–36.

Catford, J.A., Naiman, R.J., Chambers, L.E., Roberts, J., Douglas, M.M. & Davies, P. (2013) Predicting novel riparian ecosystems in a changing climate. Ecosystems, 16, 382–400.

Chen H., Qualls R.G. & Miller G.C. (2002) Adaptive responses of *Lepidium latifolium* to soil flooding: biomass allocation, adventitious rooting, aerenchyma formation and ethylene production. Environmental and Experimental Botany, 48, 119–128.

Chen, X., Huber, H., de Kroon, H., Peeters, A.J., Poorter, H., Voesenek, L.A. & Visser, E.J. (2009) Intraspecific variation in the magnitude and pattern of flooding- induced shoot elongation in *Rumex palustris*. Annals of Botany, 104, 1057–1067.

Christensen, J.H. & Christensen, O.B. (2007) A summary of the PRUDENCE model projections of changes in European climate by the end of this century. Climatic Change, 81, 7–30.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., … Whetton, P. (2007) Regional Climate Projections. In: Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, 847–940, Cambridge University Press, New York, New York.

Cirmo, C.P. & McDonnell J.J. (1997) Linking the hydrologic and biogeochemical controls of nitrogen transport in near-stream zones of temperate-forested catchments: a review. Journal of Hydrology, 199, 88-120.

Colloff, M.J., Lavorel, S., Wise, R.M., Dunlop, M., Overton, I.C. & Williams K.J. (2015) Adaptation services of floodplains and wetlands under transformational climate change. Ecological Applications, 24, 1003-1017.

Colmer, T.D., Gibberd, M.R., Wiengweera, A. & Tinh, T.K. (1998) The barrier to radial oxygen loss from roots of rice (*Oryza sativa L.*) is induced by growth in stagnant solution. Journal of Experimental Botany, 49, 1431–1436.

Cornes, R., van der Schrier, G., van den Besselaar E.J.M. & Jones P.D. (2018) An Ensemble Version of the E-OBS Temperature and Precipitation Datasets. Journal of Geophysical Research: Atmospheres, 123. 9391-9409.

Cornwell, W. K., & Ackerly, D. D. (2009) Community assembly and shifts in the distribution of trait values across an environmental gradient in coastal California. Ecological Monographs, 79, 109–126.

Craft, C.B., & Casey, W.P. (2000) Sediment and nutrient accumulation in floodplain and depressional freshwater wetlands of Georgia, USA. Wetlands, 20, 323–332.

Dai, A. (2011) Drought under global warming: a review. Wiley Interdisciplinary Reviews – Climate Change, 2, 45–65.

Dankers, R. & Feyen, L. (2009) Flood hazard in Europe in an ensemble of regional climate scenarios. Journal of Geophysical Research, 114, 16.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.C.(2011) Beyond predictions: biodiversity conservation in a changing climate. Science, 332, 53-58.

de Bello, F. & Mudrak, O. (2013). Plant traits as indicators: Loss or gain of information? Applied Vegetation Science, 16, 353–354.

De Jager, M., Kaphingst, B., Janse, E.L., Buisman, R., Rinzema, S.G.T. & Soons M.B. (2019) Seed size regulates plant dispersal distances in flowing water. Journal of Ecology, 107, 307–317.

Decamps, H. (1993) River margins and environmental change. Ecological Applications, 3, 441–445.

Díaz, S., & Cabido, M. (2001) Vive la difference: Plant functional diversity matters to ecosystem processes. Trends in Ecology & Evolution, 16, 646–655.

Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., … Band, S. R. (2004) The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science, 15, 295–304

Douma, J.C., Bardin, V., Bartholomeus, R.P. & van Bodegom, P.M. (2012) Quantifying the functional responses of vegetation to drought and oxygen stress in temperate ecosystems. Functional Ecology, 26, 1355-1365.

Douville, H., Chauvin, F., Planton, S., Royer, J. F., Salas-Melia, D. & Tyteca, S. (2002) Sensitivity of the hydrological cycle to increasing amounts of greenhouse gases and aerosols. Climate Dynamics, 20, 45–68.

Drew, M.C. (1997) Oxygen deficiency and root metabolism: Injury and acclimation under hypoxia and anoxia. Annual Review of Plant Physiology and Plant Molecular Biology, 48, 223–250.

Duursma, R. (2019) bootpredictlme4: Predict Method For lme4 With Bootstrap. R package version 0.1.

Elcan, J.M. & Pezeshki, S.R. (2002) Effects of flooding on susceptibility of *Taxodium distichum L*. seedlings to drought. Photosynthetica, 40, 177–182.

European Environment Agency (EEA) (2018) European waters, assessment of status and pressures. Kristensen, P., Whalley, C., Néry, F., Zal, N., Christiansen, T. Luxembourg: Publications Office of the European Union. https://www.eea.europa.eu/publications/state-of-water/

Feyen, L. & Dankers, R. (2009) Impact of global warming on streamflow drought in Europe. Journal of geophysical research, 114, 17.

Fischer, E.M. & Schär, C. (2010) Consistent geographical patterns of changes in high-impact European heatwaves. Nature Geoscience, 3, 398–403.

Fraaije, R.G.A., ter Braak, C.J.F., Verduyn, B.G., Breeman, L.B.S., Verhoeven, J.T.A. & Soons, M.B. (2015a) Early plant recruitment stages set the template for the development of vegetation patterns along a hydrological gradient. Functional Ecology, 29, 971–980

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

Fraaije, R.G.A. (2016) Plants living on the edge: colonization processes of aquatic and riparian vegetation along restored lowland streams. PhD thesis. Utrecht University, Utrecht, the Netherlands

Frei, C., Schöll, R., Fukutome, S., Schmidli, J. & Vidale, P.L. (2006) Future change of precipitation extremes in Europe: intercomparison of scenarios from regional climate models. Journal of Geophysical Research, 111, 22.

Froend, R. & Sommer, B. (2010) Phreatophytic vegetation response to climatic and abstraction-induced groundwater drawdown: examples of long-term spatial and temporal variability in community response. Ecological Engineering, 36, 1191–1200.

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.

Garssen, A.G., Verhoeven, J.T.A. & Soons, M.B. (2014) Effects of climate-induced increases in summer drought on riparian plant species: a meta-analysis. Freshwater Biology, 59, 1052–1063.

Geigenberger, P. (2003) Response of plant metabolism to too little oxygen. Current Opinion in Plant Biology, 6, 247–256.

Gonzalez, E., Comin, F.A. & Muller, E. (2010) Seed dispersal, germination and early seedling establishment of *Populus alba* L. under simulated water table declines in different substrates. Trees, 24, 151–163.

Goodson, J.M., Gurnell, A.M., Angold, P.G. & Morrissey, I.P. (2003) Evidence for hydrochory and the deposition of viable seeds within winter flow-deposited sediments: the River Dove, Derbyshire, UK. River Research and Applications, 19, 317–334.

Goodson, J.M., Gurnell, A.M., Angold, P.G., & Morrissey, I.P. (2003) Evidence for hydrochory and the deposition of viable seeds within winter flow-deposited sediments: The River Dove, Derbyshire, UK.

Goodson, J.M., Davenport, A., Gurnell, A.M. & Thompson, K. (2004) Hydrochory, river flow regime and riparian vegetation. Hydrology: Science & Practice for the 21st Century, 2, 99–105. British Hydrological Society International Conference from 12/07/2004 to 16/07/2004.

Greet, J., Webb, J.A., & Cousens, R.D. (2015) Floods reduce the prevalence of exotic plant species within the riparian zone: Evidence from natural floods. Applied Vegetation Science, 18, 503–512.

Gregory, J., Mitchell, J. & Brady, A. (1997) Summer drought in northern midlatitudes in a time-dependent CO_2 climate experiment. Journal of Climate, 10, 662–686.

Gregory, S., Swanson, F. J., McKee, W.A. & Cummins, K.W. (1991) An ecosystem perspective of riparian zones. BioScience, 41, 540–551.

Hautier, Y., Niklaus, P.A. & Hector, A. (2009) Competition for light causes plant biodiversity loss after eutrophication. Science, 324, 636– 638.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E.W., Borer, E.T. & Reich, P.B. (2015) Anthropogenic environmental changes impact ecosystem stability via biodiversity. Science, 348, 336–340.

Hefting, M.M. (2003) Nitrogen transformation and retention in riparian buffer zones. PhD thesis, Utrecht University, The Netherlands.

Hefting, M.M., Beltman, B., Karssenberg, D., Rebel, K., Riessen van, M. & Spijker, M. (2006) Water quality dynamics and hydrology in nitrate loaded riparian zones in the Netherlands. Environmental Pollution, 139, 143–156.

Helsen, K., Hermy, M. & Honnay, O. (2012) Trait but not species convergence during plant community assembly in restored semi- natural grasslands. Oikos, 121, 2121–2130.

Higler, L.W.G. (1993) The riparian community of North-West European lowland streams. Freshwater Biology, 29, 1993.

Hirabayashi, Y., Mahendran, R., Koirala, S., Konoshima, L., Yamasaki, D., Watanabe, S., ... Kanae, S. (2013). Global flood risk under climate change. Nature Climate Change, 3, 816–821.

Horner, G.J., Cunningham, S.C., Thomson, J.R., Baker, P.J., & Mac Nally, R. (2012) Forest structure, flooding and grazing predict understorey composition of floodplain forests in southeastern Australia. Forest Ecology and Management, 286, 148–158.

Horton, J.L. & Clark, J.L. (2000) Water table decline alters growth and survival of *Salix gooddingii* and *Tamarix chinensis* seedlings. Forest Ecology and Management, 140, 239–247.

Hough-Snee, N., Laub, B. G., Merritt, D. M., Long, A. L., Nackley, L. L., Roper, B.B., & Wheaton, J.M. (2015) Multi-scale environmental filters and niche partitioning govern the distributions of riparian vegetation guilds. Ecosphere, 6, 1–22.

Hudon, C. (2004) Shift in wetland plant composition and biomass following low-level episodes in the St. Lawrence River: looking into the future. Canadian Journal of Fisheries and Aquatic Sciences, 61, 603–617.

Hughes, J.W. & Cass, W.B. (1997) Pattern and process of a floodplain forest, Vermont, USA: predicted responses of vegetation to perturbation. Journal of Applied Ecology, 43, 594–612.

Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution, 15, 56-61.

Hussner, A., Meyer, A. & Busch, J. (2008) The influence of water level and nutrient availability on growth and root system development of *Myriophyllum aquaticum*. Weed Research, 49, 73–80.

Insausti, P., Grimoldi, A.A., Chaneton, E.J., Vasellati, V. (2001) Flooding induces a suite of adaptive plastic responses in the grass *Paspalum dilatatum*. New Phytologist, 152, 291–299.

Intergovernmental Panel on Climate Change (IPCC) (2007) Synthesis report: summary for policymakers. In: Fourth Assessment Report, IPCC Plenary XXVII, Valencia, Spain. http://www.ipcc.ch/pdf/assessment-report/ar4/wg1/ar4_wg1_full_report.pdf

Intergovernmental Panel on Climate Change (IPCC) (2013) The physical science basis. In: Fifth Assessment Report: Climate Change 2013. Cambridge University Press, Cambridge, UK. http://www.climatechange2013.org/images/report/WG1AR5_ALL_FINAL.pdf

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)(2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., Bezemer, T.M., … Eisenhauer, N. (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature, 526, 574–577.

Jackson, M.B. & Armstrong, W. (1999) Formation of aerenchyma and the processes of plant ventilation in relation to soil flooding and submergence. Plant Biology, 1, 274–287.

Janson, R., Laudon, H., Johansson, E. & Augspurger, C. (2007) The importance of groundwater discharge for plant species number in riparian zones. Ecology, 88,131–139.

Janson, R., Zinko, U., Merritt, D.M. & Nilsson, C. (2005) Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. Journal of Ecology, 93, 1094–1103.

Janson, R., Nilsson, C. & Renöfal,t B. (2000) Fragmentation of riparian floras in rivers with multiple dams. Ecology, 81, 899–903.

Janson, R., Zinko, U., Merritt, D.M. & Nilsson, C. (2005) Hydrochory increases riparian plant species richness: a comparison between a free-flowing and a regulated river. Journal of Ecology, 93, 1094–1103.

Joint Research Committee (JRC), European Union (2018) Drought in Central-Northern Europe - September 2018. JRC European Drought Observatory (EDO) http://edo.jrc.ec.europa.eu/documents/news/EDODroughtNews201809_Central_North_Europe.pdf

Jung, V., Albert, C. H., Violle, C., Kunstler, G., Loucougaray, G., & Spiegelberger, T. (2014) Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. Journal of Ecology, 102, 45–53.

Jung, V., Violle, C., Mondy, C., Hoffmann, L., & Muller, S. (2010) Intraspecific variability and trait- based community assembly. Journal of Ecology, 98, 1134–1140.

Justin, S.H.F.W. & Armstrong, W. (1987) The anatomical characteristics of roots and plant response to soil flooding. New Phytologist, 106, 465–495.

Karlsson, I.B., Sonnenborg, T.O., Seaby, L P., Jensen, K.H., & Refsgaard, J.C. (2015). Effect of a high- end CO_2-emission scenario on hydrology. Climate Research, 64, 39–54.

Kleczewski, N.M., Herms, D.A. & Bonello, P. (2012) Nutrient and water availability alter belowground patterns of biomass allocation, carbon partitioning, and ectomycorrhizal abundance in *Betula nigra*. Trees, 26, 525–533.

Kleyer, M., & Bekker, R.M. (2008) The LEDA traitbase: A database of life- history traits of the Northwest European flora. Journal of Ecology, 96, 1266–1274.

Kominoski, J.S., Shah, J.J.F., Canhoto, C., Fischer, D.G., Giling, D.P., González, E., … McElarney, Y.R. (2013) Forecasting functional implications of global changes in riparian plant communities. Frontiers in Ecology and the Environment, 11, 423–432.

Kozlowski, T.T. & Pallardy, S.G. (2002) Acclimation and adaptive responses of woody plants to environmental stresses. The Botanical Review, 68, 270–334.

Kronvang, B., Hoffmann, C.C. & Dröge, R. (2009) Sediment deposition and net phosphorus retention in a hydraulically restored lowland river floodplain in Denmark: combining field and laboratory experiments. Marine and Freshwater Research, 60, 638–646.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B. (2017) ImerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software, 82, 1–26.

Laan, P., Tosserams, M., Blom, C.W.P.M. & Veen, B.W. (1990) Internal oxygen transport in *Rumex* species and its significance for respiration under hypoxic conditions. Plant and Soil, 122, 39–46.

Laan P. & Blom C.W.P.M. (1990) Growth and survival responses of *Rumex* species to flooding and submerged conditions: the importance of shoot elongation, underwater photosynthesis and reserve carbohydrates. Journal of Experimental Botany, 41, 775–783.

Lamers, L.P.M., Tomassen, H.B.M., & Roelofs, J.G.M. (1998) Sulphate-induced eutrophication and phytotoxicity in freshwater wetlands. Environmental Science & Technology, 32, 199–205.

Lamers, L.P.M., Falla, S-J., Samborska, E.M., Dulken, I.A.R. van, Hengsten, G. van & Roelofs, J. G.M.(2002) Factors controlling the extent of eutrophication and toxicity in sulphate-polluted freshwater wetlands. Limnology and Oceanography, 47, 585-593.

Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S., Garden, D., Dorrough, J., … Bonis, A. (2007) Assessing functional diversity in the field - methodology matters!. Functional Ecology, 22, 134–147.

Lenssen, J.P.M. & de Kroon, H. (2005) Abiotic constraints at the upper boundaries of two *Rumex* species on a freshwater flooding gradient. Journal of Ecology, 93, 138–147.

Li, S., Pezeshki, S.R. & Goodwin, S. (2004) Effects of soil moisture regimes on photosynthesis and growth in cattail (*Typha latifolia*). Acta Oecologica, 25, 17–22.

Lite, S.J. & Stromberg, J.C. (2005) Surface water and groundwater thresholds for maintaining *Populus* - *Salix* forests, San Pedro River, Arizona. Biological Conservation, 125, 153–167.

Liu, J.Z., Chen, Y.N., Chen, Y.J., Zhang, N. & Li, W.H. (2005) Degradation of *Populus euphratica* community in the lower reaches of the Tarim River, Xinjiang, China. Journal of Environmental Science (China), 17, 740–747.

Lorenz, A W., & Feld, C.K. (2013). Upstream river morphology and riparian land use overrule local restoration effects on ecological status assessment. Hydrobiologia, 704, 489–501.

Lucassen, E.C.H.E.T., Smolders, A.J.P. & Lamers, L.P.M. (2005) Water table fluctuations and groundwater supply are important in preventing phosphate-eutrophication in sulphate-rich fens: consequences for wetland restoration. Plant and Soil, 269, 109-115.

Lunt, I.D., Jansen, A. & Binns, D.L. (2012) Effects of flood timing and livestock grazing on exotic annual plants in riverine floodplains. Journal of Applied Ecology, 49, 1131–1139.

Lüdecke, D. (2019a) sjlabelled: Labelled Data Utility Functions (Version 1.0.16).

Lüdecke, D. (2018b) sjmisc: Data and Variable Transformation Functions. Journal of Open Source Software, 3, 754.

Lüdecke, D (2018c) sjPlot: Data Visualization for Statistics in Social Science. R package version 2.6.2.

Mahoney, J.M. & Rood, S.B. (1991) A device for studying the influence of declining water table on poplar growth and survival. Tree Physiology, 8, 305–314.

Malmqvist, B. & Rundle, S. (2002) Threats to the running water ecosystems of the world. Environmental conservation, 29, 134–153.

Manabe, S. & Wetherald, R. (1987) Large-scale changes of soil wetness induced by an increase in atmospheric carbon dioxide. Journal of the Atmospheric Sciences, 44, 1211– 1235.

Mattingly, R.L., Herricks, E.E. & Johnston, D.M. (1993) Channelization and levee construction in Illinois: Review and implications for management. Environmental Management, 17, 781–795.

Merritt, D.M., Scott, M.L., Le Roy Poff, N., Auble, G.T., & Lytle, D.A. (2010) Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. Freshwater Biology, 55, 206–225.

Merritt, D.M. & Wohl, E.E. (2002) Processes governing hydrochory along rivers: hydraulics, hydrology and dispersal phenology. Ecological Applications, 12, 1071–1087.

Millennium Ecosystem Assessment (MEA) (2005) Ecosystems and Human Well-Being: Biodiversity Synthesis. World Resources Institute, Washington DC, U.S.A.

Mitsch, W.J., & Gosselink, J.G. (1993)Wetlands, 2nd ed. New York, NY: Van Nostrand Reinhold Company. 722 pp.

Mitsch, W.J. & Gosselink, J.G. (2015) Wetlands. 5th ed. New York, NY: Wiley. 456 pp.

Moggridge, H.L., & Gurnell, A.M. (2010) Hydrological controls on the transport and deposition of plant propagules within riparian zones. River Research and Applications, 26, 512–527.

Moggridge, H.L., Gurnell, A.M., & Mountford, J.O. (2009) Propagule input, transport and deposition in riparian environments: The importance of connectivity for diversity. Journal of Vegetation Science, 20, 465–474.

Mommer, L., De Kroon, H., Pierik, R., Bögemann, G.M., & Visser, E.J. (2005) A functional comparison of acclimation to shade and submergence in two terrestrial plant species. New Phytologist, 167, 197–206.

Naiman, R.J. & Decamps, H. (1997) The ecology of interfaces: riparian zones. Annual review of Ecology and Systematics, 28, 621–658.

Naiman, R.J., Decamps, H. & McClain, M.E. (2005) Riparia: Ecology, Conservation, and Management of Streamside Communities. Elsevier, Oxford, UK.

Naiman, R.J., Decamps, H., Pollock, M. (1993) The role of riparian corridors in maintaining regional biodiversity. Ecological Applications, 3, 209–212.

Naiman, R.J., Décamps, H., & McClain, M.E. (2005) Riparia. Ecology, Conservation, and Management of Streamside Communities. London: Elsevier Academic Press.

Naiman, R.J., & Decamps, H. (1997) The ecology of interfaces: Riparian zones. Annual Review of Ecology and Systematics, 28, 621–658.

Naiman, R.J., Decamps, H., & McClain, M.E. (2005) Riparia: Ecology, conservation, and management of streamside communities. San Diego, CA: Elsevier/Academic Press.

Naiman, R.J., Decamps, H., & Pollock, M. (1993) The role of riparian corridors in maintaining regional biodiversity. Ecological Applications, 3, 209–212.

Naiman, R.J. & Decamps, H. (1997) The ecology of interfaces: riparian zones. Annual review of Ecology and Systematics, 28, 621–658.

Naiman, R.J., Decamps, H. & Pollock, M. (1993) The role of riparian corridors in maintaining regional biodiversity. Ecological Applications, 3, 209–212.

Nakai, A., Yurugi, Y. & Kisanuki, H. (2010) Stress responses in *Salix gracilistyla* cuttings subjected to repetitive alternate flooding and drought. Trees, 24, 1087–1095.

Nakai, A., Yurugi, Y. & Kisanuki, H. (2009) Growth response of *Salix gracilistyla* cuttings to a range of substrate moisture and oxygen availability. Ecological research, 24, 1057–1065.

Nielsen, S.L. & Sand-Jensen, K. (1989) Regulation of photosynthetic rates of submerged rooted macrophytes. Oecologia, 81, 364–368.

Nilsson, C. & Grelsson, G. (1990) The effects of litter displacement on riverbank vegetation. Canadian Journal of Botany, 68, 735–741.

Nilsson, C., Brown, R.L., Jansson, R., & Merritt, D.M. (2010) The role of hydrochory in structuring riparian and wetland vegetation. Biological Reviews, 85, 837–858.

Nilsson, C., Ekblad, A., Dynesius, M., Backe, S., Gardfjell, M., Carlberg, B., Hellqvist S. & Jansson, R. (1994) A comparison of species richness and traits of riparian plants between a main river channel and its tributaries, Journal of Ecology, 82, 281 – 295.

Noe, G.B., Hupp, C.R., & Rybicky, N.B. (2013) Hydrogeomorphology influences soil nitrogen and phosphorus mineralization in floodplain wetlands. Ecosystems, 16, 75–94.

Oddershede, A., Svenning, J.C., & Damgaard, C. (2015) Topographically determined water availability shapes functional patterns of plant communities within and across habitat types. Plant Ecology, 216, 1231–1242.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., … Wagner, H. (2014) Vegan: Community ecology package. R package version 2.2-0. Retrieved from http://CRAN.R-project.org/ package=vegan.

Olde Venterink, H., Vermaat, J.E., Pronk, M., Wiegman, F., van der Lee, G.E.M., van den Hoorn, M.W., ... Verhoeven J.T.A. (2006) Importance of sediment deposition and denitrification for nutrient retention in floodplain wetlands. Applied Vegetation Science, 9, 163–174.

Olsen, S.R., Cole, C.V., Watanabe, F.S., & Dean, L.A. (1954) Estimation of available phosphorus in soils by extraction with sodium bicarbonate. USDA Circular 939. Washington, DC: US Government Printing Office.

Osenberg, C.W., Sarnelle, O. & Cooper, S.D. (1997) Effect size in ecological experiments: The application of biological models in meta-analysis. American Naturalist, 150, 799–812.

Osterkamp W.R. & Hupp C.R. (2010) Fluvial processes and vegetation - Glimpses of the past, the present, and perhaps the future. Geomorphology, 116, 274–285.

Ozinga, W.A., Bekker, R.M., Schaminee, J.H., & Van Groenendael, J.M. (2004). Dispersal potential in plant communities depends on environmental conditions. Journal of Ecology, 92, 767–777.

Pallardy, S.G. (2008) Physiology of Woody Plants, 3rd edition. The Netherlands: Academic press, Elsevier.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology Evolution and Systematics, 37, 637-669.

Pedersen, O., Rich, S.M. & Colmer, T.D. (2009) Surviving floods: leaf gas films improve O_2 and CO_2 exchange, root aeration, and growth of completely submerged rice. The Plant Journal, 58, 147–156.

Perry, L.G., Andersen, D.C., Reynolds, L.V., Mark Nelson, S. & Shafroth, P.B. (2012) Vulnerability of riparian ecosystems to elevated CO_2 and climate change in arid and semiarid western North America. Global Change Biology, 18, 821–842.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sanchez-Cordero, V., Soberon-Mainero, J., Buddemeier, R.H., & Stockwell, D.R.B. (2002) Future projections for Mexican faunas under global climate change scenario. Nature, 416, 626–629.

Petit, N.E., Froend, R.H. & Davies, P.M. (2001) Identifying the natural flow regime and the relationship with riparian vegetation for two contrasting western Australian rivers. Regulated Rivers: Research and Management, 17, 201–215.

Pezeshki, S.R. (1991) Root responses of flood-tolerant and flood-sensitive tree species to soil redox conditions. Trees, 5, 180–186.

Pezeshki, S.R. (1993) Differences in patterns of photosynthetic responses to hypoxia in flood-tolerant and flood-sensitive tree species. Photosynthetica, 28, 423–430.

Pezeshki, S.R., Anderson, P.H. & Shields, F.D. (1998) Effects of soil moisture regimes on growth and survival of black willow (*Salix nigra*) posts (cuttings). Wetlands, 18, 460–470.

Pierik, R., van Aken, J.M., Voesenek, L.A.C.J. (2009) Is elongation-induced leaf emergence beneficial for submerged *Rumex* species? Annals of Botany, 102, 353–357.

Poff, L.N., Allan, D.J., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., ... Stromberg, J. (1997) The natural flow regime. BioScience, 47, 769–784.

Pollock, M.M., Naiman, R.J. & Hanley, T.A. (1998) Plant species richness in riparian wetlands: a test of biodiversity theory. Ecological Society of America, 79, 94–105.

Poorter, L. & Markesteijn, L. (2008) Seedling traits determine drought tolerance of tropical tree species. Biotropica, 40, 321-331.

R Core Team (2018) R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/

REFRESH (2014a) Project website: http://www.refresh.ucl.ac.uk/

REFRESH (2014b) Deliverable 4.4: Summary report on the effects of climate-driven changes in temperature and hydrology on the successes of management strategies applied to riparian wetlands, particularly for restoration of wetlands and mitigation of climate change effects on catchments. http://www.refresh.ucl.ac.uk/webfm_send/2393

Renöfalt, B.M., Merritt, D.M., Nilsson, C. (2007) Connecting variation in vegetation and stream flow: the role of geomorphic context in vegetation response to large floods along boreal rivers. Journal of Applied Ecology, 44, 147–157.

Richardson, D.M., Holmes, P.M., Esler, K.J., Galatowitsch, S.M., Stromberg, J.C., Kirkman, S.P., ... Hobbs, R.J. (2007) Riparian vegetation: Degradation, alien plant invasions, and restoration prospects. Diversity and Distributions, 13, 126–139.

Riis, T., Baattrup-Pedersen, A., Poulsen, J.B. & Kronvang, B. (2014) Seed germination from deposited sediments during high winter flow in riparian areas. Ecological Engineering, 66, 103–110.

River Research and Applications, 19, 317–334.

Roelofs, J.G.M. (1991) Inlet of alkaline river water into peaty lowlands: Effects on water quality and *Stratiotes aloides* L. stands. Aquatic Botany, 39, 267–293.

Rojas, R., Feyen, L., Bianchi, A. & Dosio, A. (2012) Assessment of future flood hazard in Europe using a large ensemble of bias-corrected regional climate simulations. Journal of Geophysical Research-Atmospheres, 117, 22.

Romanello, G.A., Chuchra-Zbytniuk, K.L., Vandermer, J.L. & Touchette, B.W. (2008) Morphological adjustments promote drought avoidance in the wetland plant *Acorus americanus*. Aquatic Botany, 89, 390–396.

Rood, S.B., Pan, J., Gill, K.M., Franks, K.M., Samuelson, G.M. & Shepherd, A. (2008) Declining summer flows of Rocky Mountain rivers: changing seasonal hydrology and probable impacts on floodplain forests. Journal of Hydrology, 349, 397–410.

Roscher, C., Schumacher, J., Gerighausen, U., & Schmid, B. (2014) Different assembly processes drive shifts in species and functional composition in experimental grasslands varying in sown diversity and community history. PLoS ONE, 9, e101928.

Sabo, J.L., Sponseller, R., Dixon, M., Gade, K., Harms, T., Heffernan J., ... Welter, J. (2005) Riparian zones increase regional species richness by harboring different, not more, species. Ecology, 86, 56-62.

Salinas, M.J. & Casas, J.J. (2007) Riparian vegetation of two semi-arid Mediterranean rivers: basin-scale responses of woody and herbaceous plants to environmental gradients. Wetlands, 27, 831–845.

Sandel, B., Goldstein, L.J., Kraft, N.J., Okie, J.G., Shuldman, M.I., Ackerly, D.D., ... Suding, K.N. (2010) Contrasting trait responses in plant communities to experimental and geographic variation in precipitation. New Phytologist, 188, 565–575.

San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T. & Mauri, A. (2016) European Atlas of Forest Tree Species. Publication Office of the European Union, Luxembourg.

Sarneel, J.M., & Soons, M.B. (2012) Post-dispersal probability of germination and establishment on the shorelines of slow-flowing or stagnant water bodies. Journal of Vegetation Science, 23, 517–525.

Setter, T.L., Ellis, M., Laureles, E.V., Ella, L.S., Senadhira, D., Mishra, S.B., Sarkarung, S. & Datta, S. (1997) Physiology and genetics of submergence tolerance in rice. Annals of Botany, 79, 67–77.

Shannon, C.E. (1948) A mathematical theory of communication. The Bell System Technical Journal, 27, 379–423 and 623–656.

Silvertown, J., Araya, Y., & Gowing, D. (2015) Hydrological niches in terrestrial plant communities: A review. Journal of Ecology, 103, 93–108.

Silvertown, J., Dodd, M.E., Gowing, D.J.G. & Mountford, J.O. (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. Nature, 400, 61–63.

Sletvold, N. & Agren, J. (2012) Variation in resistance and tolerance to drought among Scandinavian populations of *Arabidopsis lyrata*. Evolutionary Ecology, 26, 559–577.

Smith, M. & Moss, J.S. (1998) An experimental investigation, using stomatal conductance and fluorescence of the flood sensitivity of *Boltonia decurrens* and its competitors. Journal of Applied Ecology, 35, 553–561.

Smith, M., Wu, Y. & Green, O. (1993) Effect of light and water-stress on photosynthesis and biomass production in *Boltonia decurrens* (Asteraceae), a threatened species. American Journal of Botany, 80, 859–864.

Smolders, A.J.P. & Roelofs, J.G.M. (1993). Sulphate-mediated iron limitation and eutrophication in aquatic ecosystems. Aquatic Botany, 46, 247–253.

Smolders, A.J.P., Lamers, L.P.M., Den Hartog, C. & Roelofs, J.G.M. (2003) Mechanisms involved in the decline of *Stratiotes aloides* L. in The Netherlands: Sulphate as a key variable. Hydrobiologia, 506–509, 603–610.

Smolders, A.J.P., Lucassen, E.C., Bobbink, R., Roelofs, J.G.M. & Lamers, L.P.M. (2010) How nitrate leaching from agricultural lands provokes phosphate eutrophication in groundwater fed wetlands: The sulphur bridge. Biogeochemistry, 98, 1–7.

Smolders, A.J.P., Lucassen, E.C.H.E.T, Bobbink, R., Roelofs J.G.M. & Lamers, L.P.M. (2010) How nitrate leaching from agricultural lands provokes phosphate eutrophication in groundwater fed wetlands: the sulphur bridge. Biogeochemistry, 98, 1-7.

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.

Soons, M.B. (2006) Wind dispersal in freshwater wetlands: knowledge for conservation and restoration. Applied Vegetation Science, 9, 271–278.

Soons, M.B., de Groot, G.A., Cuesta Ramirez, M.T., Fraaije, R.G.A., Verhoeven, J.T.A. & de Jager, M. (2016) Directed dispersal by an abiotic vector: Wetland plants disperse their seeds selectively to suitable sites along the hydrological gradient via water. Functional Ecology, 21, 499–508.

Soons, M.B. (2006) Wind dispersal in freshwater wetlands: knowledge for conservation and restoration. Applied Vegetation Science, 9, 271–278.

Soons, M.B., de Groot, G.A., Cuesta Ramirez, M.T., Fraaije, R.G.A., Verhoeven, J.T.A. & de Jager, M. (2017) Directed dispersal by an abiotic vector: Wetland plants disperse their seeds selectively to suitable sites along the hydrological gradient via water. Functional Ecology, 31, 499–508.

Stella, J.C. & Battles, J.J. (2010) How do riparian woody seedlings survive seasonal drought? Oecologia, 164, 579–590.

Stella, J.C., Battles, J.J., McBride, J.R. & Orr, B.K. (2010) Riparian seedling mortality from simulated water table recession, and the design of sustainable flow regimes on regulated rivers. Restoration Ecology, 18, 284–294.

Stevens, C.J., Dise, N.B., Mountford, J.O. & Gowing, D.J. (2004) Impact of nitrogen deposition on the species richness of grasslands. Science, 303, 1876–1879.

Ström L., Jansson R. & Nilsson C. (2012) Projected changes in plant species richness and extent of riparian vegetation belts as a result of climate-driven hydrological change along the Vindel river in Sweden. Freshwater Biology, 57, 49–60.

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.

Stromberg, J.C., Bagstad, K.J., Leenhouts, J.M., Lite, S.J. & Makings, E. (2005) Effects of stream flow intermittency on riparian vegetation of a semiarid region river (San Pedro River, Arizona). River Research and Applications, 21, 925–938.

Stromberg, J.C., Beauchamp, V.B., Dixon, M.D., Lite, S.J. &Paradzick, C. (2007) Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid southwestern United States. Freshwater Biology, 52, 651–679.

Stromberg, J.C., Hazelton, A.F., & White, M.S. (2009) Plant species richness in ephemeral and perennial reaches of a dryland river. Biodiversity and Conservation, 18, 663–677.

Stromberg, J.C., Lite, S.J. & Dixon, M.D. (2010) Effects of stream flow patterns on riparian vegetation of a semiarid river: implications for a changing climate. River Research and Applications, 26, 712–729.

Suding, K.N., Collins, S.L., & Gough, L. (2005) Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. Proceedings of the National Academy of Sciences of the United States of America, 102, 4387–4392.

Suding, K.N., Lavorel, S., Chapin, F.S., Cornelissen, J.H., Diaz, S., Garnier, E., … Navas, M.L. (2006) Scaling environmental change through the community-level: a trait based response and effect framework for plants. Global Change Biology, 14, 1125–1140.

Swenson, N.G., & Enquist, B.J. (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community- wide variation across latitude and elevation. American Journal of Botany, 94, 451–459.

Tabacchi, E. (1995) Structural variability and invasions of pioneer plant communities in riparian habitats of the middle Adour River (SW France). Canadian Journal of Botany, 73, 33–44.

ter Braak, C.J.F. & Šmilauer, P. (2012) Canoco Reference Manual and Users Guide: Software for Ordination, Version 5.0. Ithaca, NY: Microcomputer Power.

Thodsen, H., Baattrup-Pedersen, A., Andersen, H.E., Jensen, K.M.B., Andersen, P.M., Bolding, K. & Ovesen, N.B. (2014). Climate change effects on lowland stream flood regimes and riparian rich fen vegetation communities in Denmark. Hydrological Sciences Journal, 51, 1–15.

Thuiller, W., Albert, C.H., Dubuis, A., Randin, C. & Guisan, A. (2010) Variation in habitat suitability does not always relate to variation in species plant functional traits. Biology Letters, 6, 120–123.

Tilman, D. & Downing, J. (1994) Biodiversity and stability in grasslands. Nature, 367, 363-365.

Tockner, K. & Stanford, J.A. (2002) Riverine flood plains: present state and future trends. Environmental Conservation, 29, 308–330.

Touchette, B.W., Iannacone, L.R., Turner, G. & Frank, A. (2010) Ecophysiological responses of five emergentwetland plants to diminished water supply: an experimental microcosm study. Aquatic Ecology, 44, 101– 112.

van den Broek, T., van Diggelen, R. & Bobbink, R. (2005) Variation in seed buoyancy of species in wetland ecosystems with different flooding dynamics. Journal of Vegetation Science, 16, 579–586.

van der Maarel, E. (2007) Transformation of cover- abundance values for appropriate numerical treatment – Alternatives to the proposals by Podani. Journal of Vegetation Science, 18, 767–770.

van Eck, W.H.J.M., Lenssen, J.P.M., Rengelink, R.H.J., Blom, C.W.P.M. & de Kroon, H. (2005) Water temperature instead of acclimation stage and oxygen concentration determines responses to winter floods. Aquatic Botany, 81, 253–264.

van Eck, W.H.J.M., Lenssen, J.P.M., van de Steeg, H.M., Blom, C.W.P.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.

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.

van Kleef, H.H., Brouwer, E. , van der Loop, J.M.M., Buiks M. & Lucassen, E.C.H.E.T. (2017) Systeemgerichte bestrijding van watercrassula. Stichting Bargerveen, Nijmegen.

van Roosmalen, L., Sonnenborg, T.O. & Jensen, K.H. (2009) Impact of climate and land use change on the hydrology of a large-scale agricultural catchment. Water Resources Research, 45, W00A15.

Van Splunder, I., Voesenek, L.A.C.J., Coops, H., DeVries, X.J.A. & Blom, C.W.P.M. (1996) Morphological responses of seedlings of four species of *Salicaceae* to drought. Canadian Journal of Botany, 74, 1988–1995.

Verdonschot, P.F.M., Besse-Lototskaya, A. & van den Hoorn, M.W. (2001) Het effect van piekafvoeren op de levensgemeenschap in beekbovenlopen. Resultaten van twee veldexperimenten in een natuurlijke beek. Alterra Rapport, Wageningen, the Netherlands.

Verdonschot, P.F.M. & Nijboer, R.C. (2002) Towards a decision support system for stream restoration in the Netherlands: An overview of restoration projects and future needs. Hydrobiologia, 478, 131–148.

Verhoeven, J.T.A., Arheimer, B., Yin, C., & Hefting, M.M. (2006). Regional and global concerns over wetlands and water quality. Trends in Ecology & Evolution, 21, 96–103.

Verhoeven, J.T.A., Soons, M.B., Janssen, R., & Omtzigt, N. (2008) An Operational Landscape Unit approach for identifying key landscape connections in wetland restoration. Journal of Applied Ecology, 45, 1496–1503.

Verry, E.S., Dolloff, C.A. & Manning, M.E. (2004) Riparian ecotone: a functional definition and delineation for resource assessment. Water, Air, and Soil Pollution, 4, 67–94.

Vervuren, P.J.A., Blom, C.W.P.M. & de Kroon, H. (2003) Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. Journal of Ecology, 91, 135–146.

Violle, C., Bonis, A., Plantegenest, M., Cudennec, C., Damgaard, C., Marion, B., … Bouzillé, J.B. (2011) Plant functional traits capture species richness variations along a flooding gradient. Oikos, 120, 389–398.

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional!. Oikos, 116, 882–892.

Visser, E.J.W., Colmer, T.D., Blom, C.W.P.M. & Voesenek, L.A.C.J. (2000) Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. Plant, Cell and Environment, 23, 1237–1245.

Voesenek, L.A.C.J., Colmer, T.D., Pierik, R., Millenaar, F.F. & Peeters, A.J.M. (2006) How plants cope with complete submergence. New Phytologist, 170, 213–226.

Voesenek, L.A.C.J., Rijnders, J.H.G.M., Peeters, A.J.M., Van de Steeg, H.M. & De Kroon, H. (2004) Plant hormones regulate fast shoot elongation underwater: From genes to communities. Ecology, 85, 16–27.

Voesenek, L.A.C.J., Van Oorschot, F., Smits, A J.M. & Blom, C. (1993) The role of flooding resistance in the establishment of Rumex seedlings in river flood plains. Functional Ecology, 7, 105–114.

Voesenek, L.A.C.J., Rijnders, J.H.G.M., Peeters, A.J.M., van de Steeg, H.M. & de Kroon, H. (2004) Plant hormones regulate fast shoot elongation under water: from genes to communities. Ecology, 85, 16–27.

Walls, R.L. (2010) Hybridization and plasticity contribute to divergence among coastal and wetland populations of invasive hybrid Japanese knotweed s.l. (*Fallopia* spp.). Estuaries and Coasts, 33, 902–918.

Walls, R.P., Wardop, D.H., & Brooks, R.P. (2005) The impact of experimental sedimentation and flooding on the growth and germination of floodplain trees. Plant Ecology, 176, 203–213.

Wang, G. (2005) Agricultural drought in a future climate: results from 15 global climate models participating in the IPCC 4th Assessment. Climate Dynamics, 25, 739–753.

Wassen, M.J.W., Peeters ,W.H.M. & Olde Venterink, H. (2003) Patterns in vegetation, hydrology, and nutrient availability in an undisturbed river floodplain in Poland. Plant Ecology, 165, 27–43.

Weiher, E., Clarke, G.P., & Keddy, P.A. (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. Oikos, 81, 309–322.

Westoby, M. & Wright, I.J. (2006) Land- plant ecology on the basis of functional traits. Trends in Ecology & Evolution, 21, 261–268.

Westwood, C.G., Teeuw, R.M., Wade, P.M., Holmes, N.T.H. & Guyard, P. (2006) Influences of environmental conditions on macrophyte communities in drought- affected headwater streams. River Research and Applications, 22, 703–726.

Westwood, C.G., Teeuw, R.M., Wade, P.M., Holmes, N.T. & Guyard, P. (2006) Influences of environmental conditions on macrophyte communities in drought-affected headwater streams. River Research and Applications, 22, 703–726.

Wetherald, R.T. & Manabe, S. (1999) Detectability of summer dryness caused by greenhouse warming. Climatic Change, 43, 495–511.

Wetherald, R.T. & Manabe, S. (2002) Simulation of hydrologic changes associated with global warming. Journal of Geophysical Research, 107, 15.

Wickham, H. (2016) ggplot2: Elegant Graphics for Data Analysis. New York, NY: Springer-Verlag New York.

Wright, I.J., Reich, P.B. & Westoby, M. (2003) Least-cost input mixtures of water and nitrogen for photosynthesis. American Naturalist, 161, 98–111.

Wright, I.J., Reich, P.B., Cornelissen, J.H., Falster, D.S., Groom, P.K., Hikosaka, K., … Osada, N. (2005) Modulation of leaf economic traits and trait relationships by climate. Global Ecology and Biogeography, 14, 411–421.

Zwicke, M., Alessio, G.A., Thiery, L., Falcimagne, R., Baumont, R., Rossignol, N., … Picon-Cochard, C. (2013) Lasting effects of climate disturbance on perennial grassland above-ground biomass production under two cutting frequencies. Global Change Biology, 19, 3435–3448.

Summary

Stream riparian wetlands, the temporarily flooded zones along streams, form a unique type of habitat for many characteristic plant and animal species. Riparian wetlands provide a number of important ecosystem services, but are globally under threat mainly due to land use change, pollution and climate change. Lowland stream riparian wetlands are expected to be sensitive to changes in climate, especially changes in temperature and precipitation, as these wetlands are mainly rain-fed. Still, there are large uncertainties regarding the extent to which climate change will affect these ecosystems and, more specifically, their plant species diversity and composition in the near future. Extreme events with respect to drought and flooding are projected to occur more often. These extremes are expected to have significant effects on the hydrological interaction between streams and their adjacent riparian zones, thereby also influencing plant and animal dispersal and riparian plant composition, structure and abundance. Indirectly, changes in flooding and drought events will also influence plant nutrient availability, by regulating nitrogen and phosphorus cycling.

This PhD study was conducted as part of the larger European research project REFRESH 'Adaptive Strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems', funded by the European Union's 7th Framework Programme. My study aimed at identifying the main short-term effects of increased summer drought and winter flooding episodes on stream riparian plant communities. The research approach entailed both meta-analysis studies, based on quantitative studies in the literature, and full-scale field simulation experiments. Along a climate gradient ranging from Denmark to Spain, I studied the hydrological changes and biotic processes of vegetation in stream riparian zones.

In **Chapter 2** the effects of an increase in summer drought episodes on stream riparian vegetation were studied using a quantitative meta-analysis and literature study. The effects of increased drought duration and intensity on riparian plant biomass, seedling survival and plant species composition and richness were studied. This meta-analysis showed that a drought duration exceeding approximately one month strongly reduces riparian plant biomass. Also, this drought duration and high drought intensities can be detrimental for riparian seedling survival. When comparing seedling survival across well-studied riparian tree species, *Populus* and *Salix* seedlings showed a reduced survival in response to drought, in contrast to *Tamarix* seedlings, which have the ability to rapidly and expansively elongate their roots. Such adaptations to drought were shown to be crucial for the survival. Across field studies, an increase in drought

conditions rapidly led to a decline in riparian species richness and an increased presence of species adjusted to drier conditions. Specific plant traits, particularly plasticity in rooting depth, were defined as critical for species responses. The projected increase in the duration and intensity of drought periods can thus be expected to narrow the riparian wetland zone with characteristic hydric species and lead to riparian wetland species losses in the near future.

Chapter 3 focuses on a three-year field experiment in five Atlantic European lowland streams. In this comparative study we experimentally modified the hydrology of five streams across three countries (Denmark, the Netherlands and Atlantic Spain) during summer (end of June to September) to simulate the occurrence of extended drought episodes. I assessed the responses in riparian plant species richness, biomass and plant-available nitrogen and phosphorus to periods of water table declines. Our results demonstrated that a drought duration of approximately 10 weeks in Atlantic Europe under relatively mild conditions (where water was still supplied through rainfall) had a moderate impact on the stream riparian vegetation. Only in the final year of the experiments, there was a trend of a lower species richness at the drought treatment sites compared to the control sites. When considering all years, we found a significant increase in extractable soil nitrogen and a decrease in biomass with declining water tables. It is expected that severe drought periods, with high temperatures and streambeds that dry out completely, will have a much stronger impact on riparian vegetation.

Chapter 4 describes a meta-analysis aiming to synthesize globally available experimental evidence regarding the effects of increased flooding on riparian plant community composition and species richness. The aim was to make predictions of the effects of flooding with longer duration and greater depth on riparian adult plant and seedling survival, riparian plant biomass and riparian plant species composition and richness. Results showed how longer duration of flooding, greater depth of flooding and, particularly, their combination reduce seedling survival of most riparian species. We also evaluated which plant traits are of key importance for the response of riparian plant species to flooding; plant height above water level, ability to elongate shoots and plasticity in root porosity were decisive for adult plant survival and growth during longer periods of flooding. ‘Quiescence’ as well as ‘escape’ strategies proved to be successful tactics promoting riparian plant survival. A wide variation in survival (range between 0 and 100%) was found under fully submerged conditions, while plants that protruded above the water level almost all survived. Our survey showed that the projected increase in flooding episodes will result in species shifts, leading to an increase or decrease in riparian species richness depending on the nutrient, climatic and hydrological status of the catchment. Species richness generally declined at flooded sites in nutrient-rich catchments and rain-fed lowland streams, while it usually increased at sites in desert and semi-arid climate regions.

Chapter 5 focuses on the field experimental results assessing riparian vegetation changes to increased flooding. We modified the hydrology of five streams across three countries in north-western Europe during late winter/early spring over a period of 3 years to simulate the occurrence of increased flooding episodes, and compared the responses with similar control sections. 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 close to the stream) and prolonged flooding duration (6 weeks on average). An overall decline in riparian species richness was detected after 3 years of increased flooding, while riparian plant biomass increased. Extractable soil nitrogen and phosphorus increased and were 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. This experiment demonstrates that episodes of increased winter flooding can lead to strong reductions in stream riparian plant species diversity in only a three-year period.

Chapter 6 evaluates the effects of both drought and flooding simulation events, as described in Chapters 2 and 5, on plant species richness and Shannon diversity (taxonomic diversity) as well as functional trait composition. A decline in both taxonomic and functional diversity was found, most pronouncedly under flooded conditions. We found clear indications that the functional diversity of most traits also declined under flooded conditions, particularly in near-stream areas. These findings indicate that the range of successful adaptive strategies declined under flooded conditions. Fewer consistent changes in community mean trait values were identified. This might reflect a combination of different adaptive strategies that coexist in a community and a delay in mean trait response due to a slow and progressive filling of available niches, since the establishment of new species relies on time-dependent processes, such as the dispersal and establishment of species within the areas. We expect that altered precipitation patterns will have profound consequences for riparian vegetation in temperate Europe. Losses of taxonomic and functional diversity in riparian plant communities are expected and, over time, possibly also alterations in community trait characteristics.

Results from both the meta-analyses and our field experiment, showed that negative effects of increased drought and flooding episodes on riparian plant communities can rapidly take place, within a time span of 3 years. As described in **Chapter 7**, it is critical that measures are taken at the relevant locations and scales to enhance species richness and strengthen ecosystem resilience. This is important, since riparian wetlands are often already vulnerable due to changes in catchment land use or modification. In order to mitigate the effects of these extreme episodes on stream riparian wetlands, preservation or restoration of wide riparian zones should be a priority. A focus on preservation of riparian greenbelts along the entire corridors, from headwaters to mouth, is recommended. Sufficient width and length for riparian zones is needed for hydrological and biological processes, such as the storage and purification of water and requirements for species dispersal and suitable habitat. A focus on the reduction of stream, soil and groundwater nutrients is often needed in order to reach a good water quality for a robust, species-rich riparian system. All these measures should be incorporated in management plans at the stream catchment scale. Systematic monitoring of the developments of biodiversity in stream riparian ecosystems is needed, since it can help us to estimate the long-term responses of these ecosystems to climate change.

Nederlandse samenvatting

Beekbegeleidende oeverzones, oftewel beekdalen, vormen een uniek type habitat voor veel karakteristieke planten- en diersoorten. Deze beekdalen bieden verschillende belangrijke ecosysteemdiensten, maar worden wereldwijd bedreigd, voornamelijk door veranderingen in landgebruik, vervuiling en klimaatverandering. Verwacht wordt dat deze oeverzones gevoelig zijn voor veranderingen in het klimaat, met name veranderingen in temperatuur en neerslag, omdat deze systemen voornamelijk door regenwater gevoed worden. Desondanks zijn er grote onzekerheden over de mate waarin klimaatverandering in de nabije toekomst deze ecosystemen, specifiek de diversiteit en samenstelling van de beekbegeleidende plantensoorten, zal beïnvloeden. Gebeurtenissen zoals extremere perioden van droogte en overstromingen zullen naar verwachting vaker voorkomen. Van deze uitersten wordt verwacht dat ze significante effecten hebben op de hydrologische interactie tussen beken en hun aangrenzende oeverzones, waardoor ze ook de verspreiding van planten en dieren en de samenstelling, structuur en abundantie van de beekbegeleidende plantensoorten beïnvloeden. Indirect zullen veranderingen in overstromingen en droogten ook de beschikbaarheid van voedingsstoffen voor planten beïnvloeden door stikstof- en fosforcycli te reguleren.

Dit promotieonderzoek is uitgevoerd als onderdeel van het grotere Europese onderzoeksproject REFRESH ‘Adaptive Strategies to Mitigate the Impacts of Climate Change on European Freshwater Ecosystems’, gefinancierd door het zevende kaderprogramma van de Europese Unie. Mijn studie was gericht op het identificeren van de belangrijkste kortetermijneffecten van toenemende perioden van zomerdroogte en winteroverstromingen op beekbegeleidende plantengemeenschappen. De onderzoeksbenadering omvatte zowel meta-analyse onderzoeken op basis van kwantitatieve studies in de literatuur als veldsimulatie-experimenten. Langs een klimaatgradiënt van Denemarken tot Spanje, bestudeerde ik de hydrologische veranderingen en biotische processen in de vegetatie langs laaglandbeken.

In **Hoofdstuk 2** zijn de effecten van een toename van perioden van zomerdroogte op beek- en rivierbegeleidende oevervegetaties bestudeerd met behulp van een kwantitatieve meta-analyse en literatuurstudie. De effecten van toenemende duur en intensiteit van droogte op de biomassa van oeverplanten, de overleving van zaailingen en de samenstelling en soortenrijkdom van plantensoorten zijn bestudeerd. Deze meta-analyse toonde aan dat een droogteperiode van ongeveer een maand de biomassa van de oeverplanten sterk vermindert. Deze droogteduur en sterke droogte intensiteiten kunnen ook een negatief effect hebben op de overleving van zaailingen. Bij het vergelijken van de overleving van zaailingen van typische beekbegeleidende boomsoorten vertoonden *Populus* en *Salix* zaailingen een verminderde overleving in reactie op droogte, in tegenstelling tot *Tamarix* zaailingen, die het vermogen hebben om hun wortels snel en expansief te verlengen. Dergelijke aanpassingen aan droogte bleken cruciaal te zijn voor de overleving. Veldstudies toonden aan dat een toename van droogtecondities snel kan leiden tot een afname van de soortenrijkdom aan oeverplanten en een verhoogde aanwezigheid van soorten aangepast aan drogere omstandigheden. Specifieke planteigenschappen, met name plasticiteit in worteldiepte, werden gedefinieerd als kritisch voor soortresponsen. De verwachte toename van de duur en intensiteit van droogteperioden, zal naar verwachting de oeverzones met karakteristieke soorten oeverplanten versmallen en in de nabije toekomst leiden tot afnamen van typische oeversoorten.

Hoofdstuk 3 richt zich op een driejarig veldexperiment in vijf Atlantisch Europese laaglandbeken. In deze vergelijkende studie hebben we experimenteel de hydrologie van vijf beken in drie landen (Denemarken, Nederland en Atlantisch Spanje) in de zomer (eind juni tot september) aangepast om toenemende droogte te simuleren. De effecten van periodes van waterstandsdaling op soortenrijkdom, biomassa en plant-beschikbare stikstof en fosfor heb ik geanalyseerd. Onze resultaten toonden aan dat een droogteperiode van ongeveer 10 weken onder relatief milde omstandigheden (waarbij de oever nog wel door regenval gevoed werd) een matige invloed had op de oevervegetatie. Pas in het laatste jaar van de experimenten was er een trend van een lagere soortenrijkdom waarneembaar op de locaties van de droogtebehandelingen in vergelijking met de locaties in de controle situaties. Bij het beschouwen van alle jaren vonden we een significante toename met dalende waterstanden van plant-beschikbare stikstof en een afname van biomassa. Verwacht wordt dat toekomstige meer intense droogteperioden, met hoge temperaturen en beeklopen die volledig uitdrogen, een veel sterkere invloed zullen hebben op oevervegetaties.

Hoofdstuk 4 beschrijft een meta-analyse gericht op het samenbrengen van wereldwijd beschikbare experimentele informatie met betrekking tot de effecten van toenemende overstromingen op de samenstelling van rivier- en beekbegeleidende plantengemeenschappen en soortenrijkdom. Het doel was om voorspellingen te doen van de effecten van toenemende duur en intensiteit van overstromingen op de overleving van zaailingen en volwassen oeverplanten, de biomassa en de samenstelling en rijkdom van soorten oeverplanten. De resultaten toonden aan hoe langere duur van overstromingen, grotere overstromingsdiepte en in het bijzonder hun combinatie, de overleving van zaailingen van de meeste oeversoorten vermindert. We hebben ook geëvalueerd welke plantkenmerken van cruciaal belang zijn voor de reactie van oeverplantensoorten op overstromingen; planthoogte boven waterniveau, het vermogen om stengels te verlengen en plasticiteit in wortelporositeit waren bepalend voor de overleving en groei van volwassen planten gedurende langere periodes van overstroming. ‘Quiescence’ en ‘escape’ strategieën bleken succesvolle tactieken te zijn die de overleving van oeverplanten bevorderen. Een grote variatie in overleving (bereik tussen 0 en 100%) werd gevonden onder volledig onder water staande omstandigheden, terwijl planten die boven het waterniveau uitstaken bijna allemaal overleefden. Ons onderzoek toonde aan dat de verwachte toename van episodes van overstromingen zal leiden tot verschuivingen van soorten, wat leidt tot een toename of afname van de rijkdom aan oeversoorten. Dit is afhankelijk van de nutriënten-, klimatologische en hydrologische status van het stroomgebied. De soortenrijkdom nam in het algemeen af op overstroomde locaties in voedselrijke stroomgebieden en door regenwater gevoede laaglandbeken, terwijl het gewoonlijk toenam op locaties in woestijn- en semi-aride klimaatregio’s.

Hoofdstuk 5 richt zich op de veldexperimentele resultaten van een analyse van de effecten van toenemende overstromingen op veranderingen in de oevervegetatie. We hebben de hydrologie van vijf beken in drie landen in Noordwest-Europa tijdens de late winter / vroege lente gedurende een periode van 3 jaar aangepast om een toenemende winteroverstroming te simuleren, en de reacties vergeleken met vergelijkbare controlesecties. We hebben de effecten van een verhoogde overstromingsdiepte (gemiddeld +18 cm dicht bij de beek) en verlengde overstromingsduur (gemiddeld 6 weken) op plantensoortenrijkdom, biomassa, plant-beschikbare stikstof en fosfor en zaaddeposities geanalyseerd. Een algehele afname van de rijkdom aan oeversoorten werd gedetecteerd na 3 jaar van toenemende overstromingen, terwijl de biomassa van de vegetatie toenam. De plant-beschikbare stikstof en fosfor in de bodem namen toe en droegen waarschijnlijk bij aan de toegenomen biomassa. Toenemende overstromingen resulteerden in de depositie van meer zaden van extra soorten op de oeverzone, waardoor mogelijk de verschuivingen in de samenstelling van oeverplantensoorten die we hebben waargenomen, worden vergemakkelijkt. Dit experiment toont aan dat een toename van winteroverstromingen in slechts drie jaar tijd kan leiden tot een significante afname van de diversiteit aan beekbegeleidende plantensoorten.

Hoofdstuk 6 evalueert de effecten van zowel droogte- als overstromingssimulatie-experimenten, zoals beschreven in hoofdstuk 2 en 5, op plantensoortenrijkdom en Shannon-diversiteit (taxonomische diversiteit), evenals de samenstelling van functionele plantkenmerken. Er is een afname van zowel taxonomische als functionele diversiteit gevonden, het meest uitgesproken bij de overstroomde omstandigheden. We vonden duidelijke aanwijzingen dat de functionele diversiteit van de meeste planteigenschappen ook afnam onder invloed van overstromingen, met name op plekken dichter bij de beek. Deze bevindingen geven aan dat het aantal succesvolle adaptieve strategieën afnam onder invloed van overstromingen. Er werden echter minder consistente veranderingen geïdentificeerd in de gemiddelde waarden van de gemeenschap. Dit kan een combinatie zijn van verschillende adaptieve strategieën die binnen een gemeenschap naast elkaar bestaan en een vertraging in de gemiddelde respons van plantkenmerken. Dit kan het gevolg zijn van een langzame en progressieve invulling van beschikbare niches, aangezien de komst van nieuwe soorten afhankelijk is van tijdsafhankelijke processen, zoals de verspreiding en vestiging van soorten in de gebieden. We verwachten dat veranderende neerslagpatronen ingrijpende gevolgen zullen hebben voor oevervegetaties in gematigd Europa. Afname van taxonomische en functionele diversiteit in beekbegeleidende gemeenschappen worden verwacht en, na verloop van tijd, mogelijk ook wijzigingen in kenmerken van plantengemeenschappen.

Resultaten van zowel de meta-analyses als onze veldexperimenten toonden aan dat negatieve effecten van toenemende droogte en overstromingen op beekbegeleidende vegetaties snel kunnen plaatsvinden, binnen een tijdsbestek van 3 jaar. Zoals beschreven in **Hoofdstuk 7** is het van cruciaal belang dat maatregelen worden genomen op de relevante locaties en niveaus om de soortenrijkdom te verhogen en de veerkracht van het ecosysteem te vergroten. Dit is belangrijk, omdat beek- en rivierdalen vaak al kwetsbaar zijn door veranderingen in landgebruik of modificatie van stroomgebieden. Om de effecten van deze extreme episoden op beekbegeleidende zones te verminderen, vormen behoud en/of herstel van brede oeverzones een eerste vereiste. Een focus op het behoud van brede oeverzones langs de hele beekloop, van bovenloop tot monding, wordt aanbevolen. Voldoende breedte en lengte voor oeverzones is nodig voor hydrologische en biologische processen, zoals de opslag en zuivering van water, en vereist voor de verspreiding van soorten en geschikte habitats. Ten tweede is een focus op de vermindering van nutriënten in beek-, bodem- en grondwater vaak nodig om een goede waterkwaliteit te bereiken voor een robuust, soortenrijk beekdalsysteem. Deze maatregelen tezamen dienen deel uit te maken van beheersplannen op stroomgebiedsniveau. Systematische monitoring van de ontwikkelingen van de biodiversiteit in beekdalen is nodig, omdat dit ons kan helpen in te schatten wat de langetermijnreacties van deze ecosystemen op klimaatverandering zullen zijn.

Dankwoord

Met dankbaarheid denk ik terug aan de periode waarin dit proefschrift tot stand is gekomen. Vele personen hebben gedurende dit traject een rol gespeeld en wil ik hiervoor bedanken.

Merel en Jos, jullie zijn nauw bij mijn promotieonderzoek betrokken geweest. Merel, veel dank voor de prettige samenwerking. Jouw suggesties, kritische blik en enthousiasme heb ik zeer op prijs gesteld. Jos, dank voor je nauwe betrokkenheid bij mijn onderzoek, het project REFRESH en je positiviteit. Ik ben blij dat we ook in de eindfase samen zijn opgetrokken. Ik heb veel van jullie beiden geleerd.

De samenwerking met vele internationale collega's binnen het bredere onderzoeksproject REFRESH is onvergetelijk. Mooie herinneringen komen boven wanneer ik terugdenk aan de gesprekken, de veldbezoeken en bijeenkomsten in Turkije, Spanje, Schotland, Nederland, Duitsland en Denemarken. Veel inspiratie heb ik opgedaan, ik ben dankbaar dat ik dit heb mogen meemaken. In het bijzonder wil ik de volgende collega onderzoekers danken voor de prettige en waardevolle samenwerking: Martin Kernan, Piet Verdonschot, Agata van Oosten-Siedlecka, Carl Christian Hoffmann, Annette Baattrup-Pedersen, Tenna Riis, Esben Astrup Kristensen, Isabel Pardo, Liliana García, Eugènia Marti Roca, Francesc Sabater, Armin Lorenz, Stefano Larsen, Victor Beumer, Valesca Hareslak en Bart Raven.

Tijdens mijn onderzoek heb ik studenten mogen begeleiden die een bijdrage hebben geleverd aan dit onderzoek. Een bijzondere dank aan de studenten die hebben geholpen bij de uitvoering van het veld- en labwerk. De inspanning die het vergde voor het doen slagen van het overstromingsexperiment, de tijdrovende determinatie van zaden onder de microscoop, het nauwgezet volgen van zaailingen in het veld met een speciale methode.. Doorzettingsvermogen was daarbij een vereiste. Niek, Edwin, Robin, Maikel, Annelon, Mark en John, jullie hebben goede resultaten behaald. Daarnaast heb ik een aantal studenten begeleid bij het schrijven van een scriptie: Inger, Peter, Iris en Hidde. Het was een mooie en gezellige tijd.

Dank aan de mensen van Waterschap Vallei en Veluwe. Waterschap Aa en Maas, Emschergenossenschaft/Lippeverband, Staatsbosbeheer, Natuurmonumenten en diverse terreineigenaren voor het mogelijk maken van de experimenten en jullie informatie.

Mijn oud collega's van de Ecologie en Biodiversiteit groep wil ik bedanken voor de fijne tijd. Kamergenoten Rob en Erik, we hebben veel gedeeld samen. Het was ook gezellig met mijn overige kamergenoten Simone, Peter, Liang en Shouli, Violeta en Shilei. Edwin, je statistische hulp in de eindfase was zeker welkom. Boudewijn, Heinjo, Bertus, Riks, Gerrit, Betty, Peter, Mariet, Marijke, Yann, Alexandre, Mohammadhosein, Joost, Monique en Karlijn, fijn dat we zoveel konden uitwisselen. Tot slot, George, dank voor het commentaar op een artikel. Je optimistische houding en vertrouwen heb ik gewaardeerd.

Mijn speciale dank aan mijn collega's van de provincie Overijssel. Marc, die me op positieve wijze heeft aangemoedigd het schrijven weer op te pakken en Laura, Arnold, Bastiaan, Marien, Elles, Obe, Ben, Lieveke, Paul, Emy, Piet, Herbert, Amar, Elselien, Frank, Annet, Harro, Reinder, Bauke, Ruben, Henry, Wijtze, Anna, Wicher, Remco, Hennie en collega's, dank voor jullie betrokkenheid.

Mijn familie en vriendinnen, jullie zijn mij door de jaren heen enorm van steun geweest. Mam, de liefde voor de natuur heb je me met de paplepel ingegoten. Samen met pap heb je me gestimuleerd mijn hart te volgen. Hélène, dank voor je betrokkenheid. De mooie zussenuitjes gaan we gauw weer oppakken. Dank ook aan Martin, Léon, Florieke, Hugo, Conny & Ben, overige familieleden en mijn schoonfamilie voor de fijne momenten. Anja en Maaike, we zijn al vriendinnen sinds de masteropleiding. Ik ben blij dat we deze mijlpaal in goede gezondheid kunnen vieren. Cathalina, ik ben dankbaar voor onze bijzondere vriendschap en het samen delen. Jaouad, je bent al sinds de eindfase van mijn studentenperiode in mijn hart. Dank dat je me zo steunde en voor de kopjes thee en koekjes tijdens het schrijven in de avonduren.

Tot slot, mijn lieve dochters Amana en Alisa, jullie inspireren en verrassen me keer op keer. Mijn dankbaarheid gaat uit naar jullie.

Author's affiliations

Merel B. Soons – Jos T.A. Verhoeven – Laurentius A.C.J. Voesenek – Edwin T. Pos – Bart M. Raven
Ecology & Biodiversity group, Institute of Environmental Biology, Utrecht University, Utrecht, The Netherlands

Carl C. Hoffmann – Annette Baattrup-Pedersen – Tenna Riis
Department of Bioscience, Aarhus University, Silkeborg, Denmark

Isabel Pardo – Liliana García
Department of Ecology and Animal Biology, University of Vigo, Vigo, Spain

Publications

Baattrup-Pedersen, A., **Garssen, A.G.**, Göthe, E., Hoffmann, C.C., Oddershede, A., Riis, T., van Bodegom, P.M., Larsen, S.E. & Soons, M.B. (2018) Structural and functional responses of plant communities to climate change-mediated alterations in the hydrology of riparian areas in temperate Europe. Ecology and Evolution, 8, 4120–4135.

Garssen, A.G., Baattrup-Pedersen, A., Riis, T., Raven, B.M., Hoffman, C.C., Verhoeven, J.T.A. & Soons, M.B. (2017) Effects of increased flooding on riparian vegetation: Field experiments simulating climate change along five European lowland streams. Global Change Biology, 23, 3052–3063.

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.

Garssen, A.G., Verhoeven, J.T.A. & Soons, M.B. (2014) Effects of climate-induced increases in summer drought on riparian plant species: a meta-analysis. Freshwater Biology, 59, 1052–1063.

Wubs, E.R.J., Fraaije, R.G.A., de Groot, G.A., Erkens, R.H.J., **Garssen, A.G.**, Kleyheeg, E., Raven, B.M. & Soons, M.B. (2016) Going against the flow: a case for upstream dispersal and detection of uncommon dispersal events. Freshwater Biology, 61, 580–595.

About the author

Annemarie Garssen was born on 9 September 1982 in Vorden, the Achterhoek, a region in the eastern Netherlands. Nature is her most important source of inspiration, throughout her personal life and career. In 2000, she graduated from secondary school in Zutphen. After having spent a year abroad, working as a wildlife volunteer at several nature reserves in Costa Rica, she started in 2001 with her bachelor studies in Biology at Utrecht University. Becoming fascinated by the functioning of wetlands, she investigated the effects of water storage on groundwater-dependent wetlands in her bachelor's thesis. As part of her master degree in Natural Resources Management at Utrecht University she conducted a research internship at the Landscape Ecology Group where she investigated the effects of inundation with sulphate-enriched surface water on groundwater dependent wetlands. Her second internship was completed in the applied field of nature and wildlife conservation at the foundation Bears in Mind, Ouwehands Dierenpark, Rhenen, and partly abroad at the non-profit organization NACRES, Centre for biodiversity conservation and research in the Caucasus region.

Annemarie started her job career as Secretary of the Working Group Ecology and Development at the International Union for Conservation of Nature, the Netherlands, in Amsterdam. Here she organized several seminars and continued working as a Project Officer for the Ecosystem Grants Programme. Since she wanted to gain more in-depth knowledge of wetland functioning, she applied for a PhD position at Utrecht University, part of the REFRESH project. She took her place at the Ecology and Biodiversity Group in 2010, under supervision of Merel Soons and Jos Verhoeven. In the four years of her appointment as PhD candidate at Utrecht University, she performed two meta-analyses and carried out two large-scale field manipulations of stream drought and flooding in collaboration with other scientists, students, water boards and land owners.

In 2017 she obtained a new job as an Ecologist at the Province of Overijssel. Since the end of 2018 she continued working part-time on her PhD thesis which was submitted in August 2019. Currently, Annemarie works at the provincial department of Nature and Environment where she focusses on conservation and restoration of Natura 2000 areas and protected species in Overijssel.