

RESEARCH REVIEW

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

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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).

Keywords: biodiversity, climate change, floods, global change, hydrological changes, literature survey, riparian gradient, survival, vegetation, wetlands

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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 & Décamps, 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 & Décamps, 1997; Naiman *et al.*, 2005). Riparian ecosystems are diverse, dynamic and complex habitats (Naiman *et al.*, 1993; Naiman & Décamps, 1997); they are highly sensitive to changes in catchment land use and are among the most degraded and impacted

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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.*, 2015). 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.*, 2015). 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.*, 2015).

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 & Décamps, 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 (Baatrup-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 (Garsen *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 S1) and supplemented these with relevant cases from publications selected in an earlier analysis on the effects of drought on riparian plants (Garsen *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 S7).

Results

In total, 1205 publications emerged from our search query in Web of Science (Table S1). 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 S2), 21 reported on the effects of flooding on plant total biomass (Table S3), and 22 reported on the effects of flooding on species richness and/or species composition (Table S6). 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 S5.

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. 1a; *t*-test: $P < 0.0001$) and adult plant survival (Fig. 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 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. 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. 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 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. 1c; $N = 10$ species, 42 cases for adult plant survival, Fig. 1d; Table 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. 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 2).

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. 3c).

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. 2b), while plants with leaf parts in the air showed a wide range of responses, from severe losses to even enhanced growth (Fig. 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

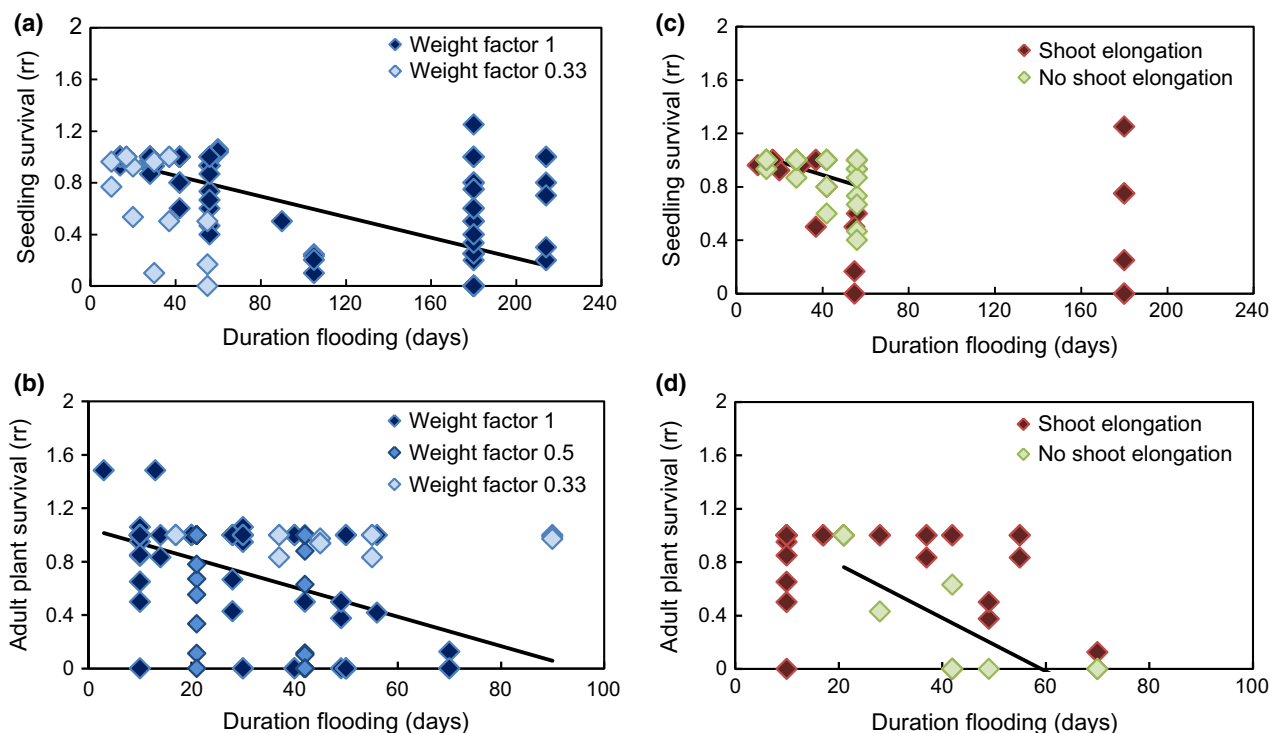


Fig. 1 Effects of duration of flooding on the response ratio of seedling survival (a, c) and adult plant survival (b, d) for different riparian species (mean number of seedlings or adult plants in treatment/seedlings or adult plants in control). Weighted regression analyses are shown. Weight factors are 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.

Table 1 Equations, R^2 and P -values of regression lines of data points in the respective figures

Figure	Equation	R^2 value	P value
1a	$y = -0.004x + 1.016$	0.433	<0.0001
1b	$y = -0.011x + 1.047$	0.203	<0.0001
1c	$y = -0.005x + 1.090$	0.251	0.001
1d	$y = -0.020x + 1.182$	0.646	0.054
2a	$y = -0.007x + 0.514$	0.126	<0.0001
2b	$y = 0.004x + 0.840$	0.232	0.002
	$y = 0.523 + 0.079 \ln(x)$	0.102	0.050
		(not shown)	
3a	$y = -0.001x + 0.538$	0.014	0.189
3b	$y = 0.021 + 0.149 \ln(x)$	0.122	0.003
3c	$y = 0.018x + 0.762$	0.249	<0.0001
3d	$y = -1.148 + 0.488 \ln(x)$	0.461	0.031

shoots, this relation was N.S.; Fig. 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 2).

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, 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 S5).

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

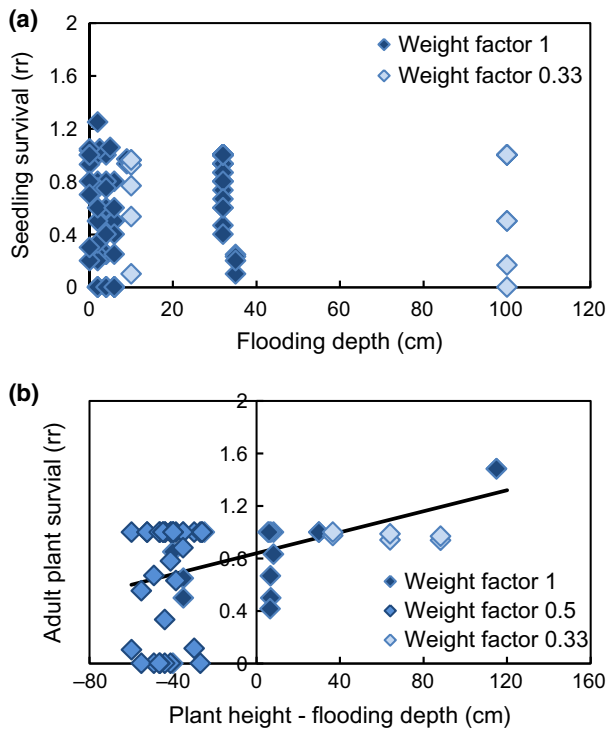


Fig. 2 Response ratio of survival (mean number of seedlings or adult plants in treatment/seedlings or adult plants in control) in relation to flooding depth (for seedlings) or in relation to relative plant height (plant height minus flooding depth) for adult plants. Weighted regression analyses are shown (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 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	-0.007	0.010
Relative plant height*duration	4.562E-005	0.333
(c) Coefficients		
Relative plant height	-0.014	0.008
Duration	-0.004	0.055
Relative plant height*duration	0.000	0.027

species composition contained nine publications reporting a decrease in species richness, seven reporting an increase and two reporting no significant effect (Table

S7). 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; Renöfält *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.

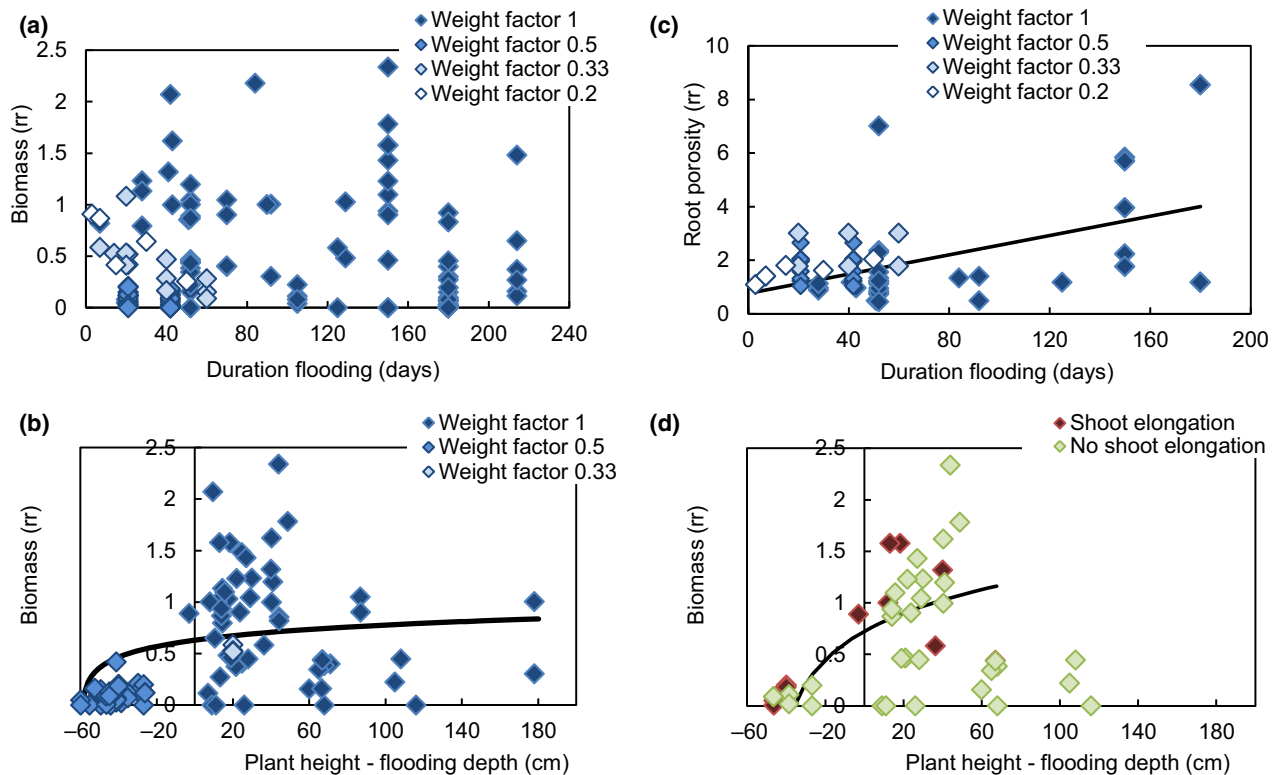


Fig. 3 Riparian adult plant biomass response ratio (mean biomass in flooding treatment/mean biomass in control) in relation to duration (a) and relative plant height (plant height minus flooding depth) (b, d). Response ratio of root porosity (mean root porosity in flooding treatment/mean root porosity 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.

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 (Renöfält *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 (Renöfält *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 (Baatrup-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.

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Supporting Information

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

- Table S1.** Keyword strings and results.
- Table S2.** Papers meta-analysis survival.
- Table S3.** Papers meta-analysis biomass.
- Table S4.** Morphological adjustments to flooding stress.
- Table S5.** List of species included in the analyses, with species growth form and relevant traits.
- Table S6.** Papers species richness.
- Table S7.** Summary of the main effects of flooding on riparian plant species richness and composition.