

Ecological assessment of the effects of hydrology  
and flooding events on floodplain meadow species  
and their potential habitats

Dissertation

for the degree

Doctor rerum naturalium (Dr. rer. nat.)

submitted by

Johannes Paul Gattringer, Bakk. rer. nat. MSc

Justus Liebig University Giessen

Giessen, July 2018

The research reported in this thesis was carried out at:

Division of Landscape Ecology and Landscape Planning  
Research Centre for Biosystems, Land Use and Nutrition (iFZ)  
Justus Liebig University Giessen, Germany

Supervisor:

Prof. Dr. Dr. habil. Dr. h. c. (TSU) Annette Otte  
Division of Landscape Ecology and Landscape Planning  
Research Centre for Biosystems, Land Use and Nutrition (iFZ)  
Justus Liebig University Giessen

Second supervisor:

Prof. Dr. Volkmar Wolters  
Department of Animal Ecology and Systematics  
Research Centre for Biosystems, Land Use and Nutrition (iFZ)  
Justus Liebig University Giessen

# Contents

	List of publications	4
<b>Chapter 1</b>	Ecological assessment of the effects of hydrology and flooding events on floodplain meadow species and their potential habitats: a synthesis	5
<b>Chapter 2</b>	Flooding tolerance of four floodplain meadow species depends on age	32
<b>Chapter 3</b>	Interaction between depth and duration matters: flooding tolerance of 12 floodplain meadow species	54
<b>Chapter 4</b>	Modeling of rare flood meadow species distribution by a combined habitat-surface water-groundwater model	77
	Abstract	105
	Zusammenfassung	106
	Acknowledgements	107
	Declaration	108

# List of publications

This thesis is based on the following three papers:

- 1) Gattringer JP, Donath TW, Eckstein RL, Ludewig K, Otte A, Harvolk-Schöning S (2017) Flooding tolerance of four floodplain meadow species depends on age. *PLoS ONE* 12:e0176869. doi: 10.1371/journal.pone.0176869
- 2) Gattringer JP, Ludewig K, Harvolk-Schöning S, Donath TW, Otte A (2018) Interaction between depth and duration matters: flooding tolerance of 12 floodplain meadow species. *Plant Ecology* 219:973–984. doi: 10.1007/s11258-018-0850-2 #
- 3) Gattringer JP\*, Maier N\*, Breuer L, Otte A, Donath TW, Kraft P, Harvolk-Schöning S (submitted manuscript) Modeling of rare flood meadow species distribution by a combined habitat-surface water-groundwater model.

For the first and second paper, I had the main responsibility for conceptualization, data analysis, and writing. I conducted most of the experimental work. For the third paper, N. Maier and I contributed equally to the work and we both had the main responsibility, including conceptualization of the study and writing. I conducted most of the ecological fieldwork, the statistical habitat modeling and analysis. N. Maier computed the hydrological modeling and collected hydrological field data. All co-authors contributed constructive suggestions and helpful comments.

Furthermore, I contributed to the conceptualization, data analysis, and writing of the following article:

- 4) Volk XK, Gattringer JP, Otte A, Harvolk-Schöning S (2018) Connectivity analysis as a tool for assessing restoration success. *Landscape Ecology* 33:371–387. doi: 10.1007/s10980-018-0611-6

# Reprinted by permission from Springer Nature © 2018

\* These authors contributed equally to the work

# CHAPTER 1

## Ecological assessment of the effects of hydrology and flooding events on floodplain meadow species and their potential habitats: a synthesis

### Introduction

#### *Floodplain meadow species*

Natural floodplains serve as regional biodiversity hotspots since they are characterized by an unusual high diversity of species and environmental processes (Naiman et al. 1993; Tockner and Stanford 2002). For centuries, floodplain ecosystems have been strongly influenced by human actions such as river regulation (Giller and Malmqvist 1998). As a consequence, floodplain habitats are among the most threatened habitat types in Central Europe (Joyce and Wade 1998; Finck et al. 2017). These habitats harbor numerous rare and endangered species and thus are of high nature conservation value (Tockner and Stanford 2002). In particular, species-rich floodplain meadows of the plant community *Cnidion dubii* (Burkart et al. 2004) have been in the focus of conservationists for decades (Kiehl et al. 2010). The big part of these meadows was converted to arable land or transferred to intensive land management (e.g., increased cutting frequency, fertilizer application) during the 20<sup>th</sup> century (Joyce and Wade 1998). Nowadays, only few remnants of the floodplain meadows still occur along the river valleys of Europe's large rivers; for example along the Rhine, Danube, and Elbe Rivers (Burkart 2001) and thus are protected throughout Europe (EU Habitats Directive; Council Directive 92/43/EEC Annex I; habitat type 6440: alluvial meadows of river valleys of the *Cnidion dubii*). Therefore, numerous restoration campaigns focused on the restoration of these meadows and therewith on the reestablishment of the often endangered plant species they harbor (e.g., Donath et al. 2007; Kiehl et al. 2010; Engst et al. 2016). However, restoration success was not equally

high on all target sites due to the complex habitat requirements of the floodplain meadow species (Donath et al. 2003; Harnisch et al. 2014).

These floodplain meadow species are a set of plant species that grow predominantly (or exclusively) along large rivers in Central European lowlands. Interestingly, this observed distribution pattern is a biogeographic description as the plants show a high ecological heterogeneity owing to the great diversity of environmental processes in riparian grassland (Burkart 2001). In general, only little is known about the mechanism that cause the biogeographic distribution pattern of the floodplain meadow species. Therefore, experimental studies that reveal the autecological characteristics of species are particularly necessary (Burkart 2001). Several studies already focused on the experimentally testing of hypothesis to investigate possible functional traits (Geissler and Gzik 2008; Burmeier et al. 2010; Burmeier et al. 2011; Ludewig et al. 2014b; Hanke et al. 2014; Ludewig et al. 2018). Up to now, a grouping based on functional traits of the species still is missing. In order to improve the conservation planning of floodplain meadow species and for the understanding of this particular distribution pattern, determining a functional grouping is essential (Burkart 2001). Investigating functional traits has been on the agenda for researchers for decades, since floodplain meadow plants possess manifold strategies to tolerate the specific conditions in floodplains; they are able to cope with the complex hydrological and disturbance regimes, such as the interplay of flooding and drought (Burkart 2001).

#### *The role of hydrology and flooding*

Today, floodplain meadow vegetation is mainly shaped by land use and hydrological conditions, which represent the key disturbance factors in recent riparian grassland (Giller and Malmqvist 1998; Bunn and Arthington 2002; Ludewig et al. 2014a). River regulation has led to significant changes in water regime (e.g., reduced water level fluctuations) with substantial alterations of species composition and spatial distribution of floodplain plants (Leyer 2005). Nevertheless, the strong interannual variation of flood and drought is still an important driver of vegetation dynamics in floodplain meadows (Mathar et al. 2015). Drought stress affects grassland communities often by reducing plant growth (Gilgen and Buchmann 2009) and also drought duration and frequency seem to determine plant zonation in floodplain meadows (Ludewig et al. 2018). Regular flooding influences the distribution and diversity of floodplain plant species in several ways (Malanson 1993); it facilitates the recruitment of less competitive species by the formation of bare soil for germination niches and inhibits flood-sensitive competitors (Hölzel and Otte 2004). Thereby, flooding maintains the diver-

sity of rare species through the recruitment of seedlings from the soil seed bank (Hölzel and Otte 2001).

As a consequence of the ecological heterogeneity of the floodplain meadow species, on a micro-habitat scale, these plants segregate in accordance to their hydrological niches (Silvertown et al. 1999; Silvertown et al. 2015); flood sensitive species occupy elevations, whereas flood tolerant species occur in depressions (Vervuren et al. 2003; Jung et al. 2008). This microhabitat preference could even be detected in differing germination strategies in floodplain meadow species indicative of wet or dry habitats (Ludewig et al. 2014b). Accordingly, it seems clear that plants are sensitive to hydrology at a fine scale (Silvertown et al. 1999). The microrelief, which is primarily the result of riverine sedimentation through flooding (Malanson 1993), leads to strong differences in hydrological conditions on a micro-habitat scale (e.g., flooding depth and duration) with little-known consequences to plants.

In general, but also specifically for floodplain meadow species, flooding represents a phenomenon with multiple components that all influence plant growth (Vervuren et al. 2003). Among those components, the timing, duration and depth of a flooding event are the key factors affecting plant growth in riparian ecosystems (besides several other components, e.g., flooding frequency, floodwater temperature, and suspended load) (Cronk and Fennessy 2001; Vervuren et al. 2003; Magee and Kentula 2005). The timing of a flooding event (i.e., when the flooding event occurs, e.g., winter or summer) is known to influence plant growth and plant diversity in wetland ecosystems (Greet et al. 2011; Webb et al. 2012). In floodplain meadows, predominantly summer floods determine plant zonation, as summer floods have a stronger impact on vegetation than winter floods (Van Eck et al. 2006). Besides, the timing in terms of plant age during flooding is also a decisive factor; mature plants cope better with floods than juveniles (Nabben et al. 1999). The component flooding duration is generally regarded as an important factor for floodplain habitats. Cumulative flooding days per year is the common parameter to deduce plant distribution patterns in floodplains and is used, for example, for predicting the transition zone between hardwood and softwood floodplain forests (Ellenberg 2009). Studies of floodplain meadow species detected that plant survival and growth decreases with increasing flooding duration (Blom et al. 1994; Van Eck et al. 2004). Also the component flooding depth has severe consequences on plant performance; increasing flooding depth reduces survival and biomass production of floodplain grassland species (Mauchamp et al. 2001; Vervuren et al. 2003). However, interactive effects of the mentioned flooding components have rarely been studied, although they seem to be of particular importance to plant growth (Madsen and Sand-Jensen 1994; Van Eck et al. 2005). Regarding the restora-

tion of floodplain meadow species, the detailed knowledge of the flooding tolerance of target species is of particular importance in restoration planning and should also be integrated when assessing habitat suitability of potential target sites.

#### *Assessment of habitat suitability*

Taking the above-mentioned aspects into consideration, flooding events as well as the hydrological conditions in general seem to have a complex role in the reestablishment of floodplain meadow species and thus in restoration management (Bissels et al. 2004). The habitat requirements of target species might not match with the site conditions if those factors are neglected during target site selection. In this regard, detailed habitat-suitability analyses of target species that incorporate the complex environmental conditions (i.e., hydrological situation) could enhance restoration planning (Guisan et al. 2013).

Such habitat models are the most common method to obtain spatially explicit predictions of environmental suitability for species (Guisan and Thuiller 2005; Elith and Leathwick 2009; Peterson et al. 2011; Guisan et al. 2017). Therefore, mainly statistical relationships between the species observations and their environmental descriptors are analyzed in order to quantify the range of suitable habitat conditions for the species (Guisan et al. 2017). This step represents the calibration of the model. In a next step, this fitted habitat-suitability model is evaluated, mostly in terms of a split-sampling procedure. In practice, those two steps are often combined and the model is calibrated with 80% of the data and evaluated over the remaining 20% for multiple times (Peterson et al. 2011). This enables to calculate model quality indices such as the area under the receiver operating characteristic curve (AUC) (Hanley and McNeil 1982) or the true skills statistic (TSS) (Allouche et al. 2006), which assess the accuracy for the predictions of the model in comparison to the actual situation. Finally, the model is used to calculate a spatial projection of the model in geographic space based on maps of the environmental predictors. This projection represents the species' potential distribution (Guisan et al. 2017).

In the last decades, habitat modeling has become a common tool in biodiversity management. Still, the modeling of rare and endangered species was regarded as a challenge for a long time (Guisan and Thuiller 2005; Elith and Leathwick 2009). Datasets of rare and endangered species often have only few occurrence records. To sufficiently include the key environmental conditions in the species model, mostly a high number of explanatory variables (i.e., predictors) is necessary. That might lead to model overfitting, if too many predictors for the limited number of available observations are included (Guisan and Zimmermann 2000). The overfitting may result in



decreased generalizability of the models and thus should be avoided (Vaughan and Ormerod 2005). In the last years, several novel approaches to overcome this obstacle were proposed (e.g., Lomba et al. 2010; Shcheglovitova and Anderson 2013; Breiner et al. 2015). In particular, the method described by Breiner et al. (2015; 2018) is promising; this method is based on building an ensemble model of several small bivariate models (ensembles of small models, ESM). This procedure avoids overfitting without reducing the number of predictor variables and thus without the loss of explanatory power. Recently, Di Febbraro et al. (2017) have shown that the ESM strategy is a beneficial approach in their modeling of rare megafaunal species. The ESM approach is able to improve the reliability of SDMs of rare and endangered species and can thus support conservation decisions (Breiner et al. 2018).

For floodplain vegetation modeling, few studies have tested the integration of hydrological information into habitat models (Leyer 2005; Büchele et al. 2006; Mosner et al. 2011; Mosner et al. 2015). However, until now, only simple hydrological variables have been considered in habitat models – studies that incorporate detailed hydrological parameters with high spatial and temporal resolution are not at hand. Such models should provide higher accuracy and thus better predictability of habitat suitability for restoration target species. That could facilitate target site selection and, correspondingly, cost efficiency of floodplain meadow restoration projects.

## Objectives

In summary, the described background underlines that flooding and the hydrological conditions have substantial influence on the establishment of floodplain meadow species and, therewith, on floodplain restoration. Since the mechanisms that cause the species' distribution pattern are still unknown, this thesis aims at gaining a deeper understanding of the factors hydrology and flooding in this context. I present experiments and a subsequent analysis of the effects of the hydrological situation on the ecology, distribution, and habitat suitability of this species group.

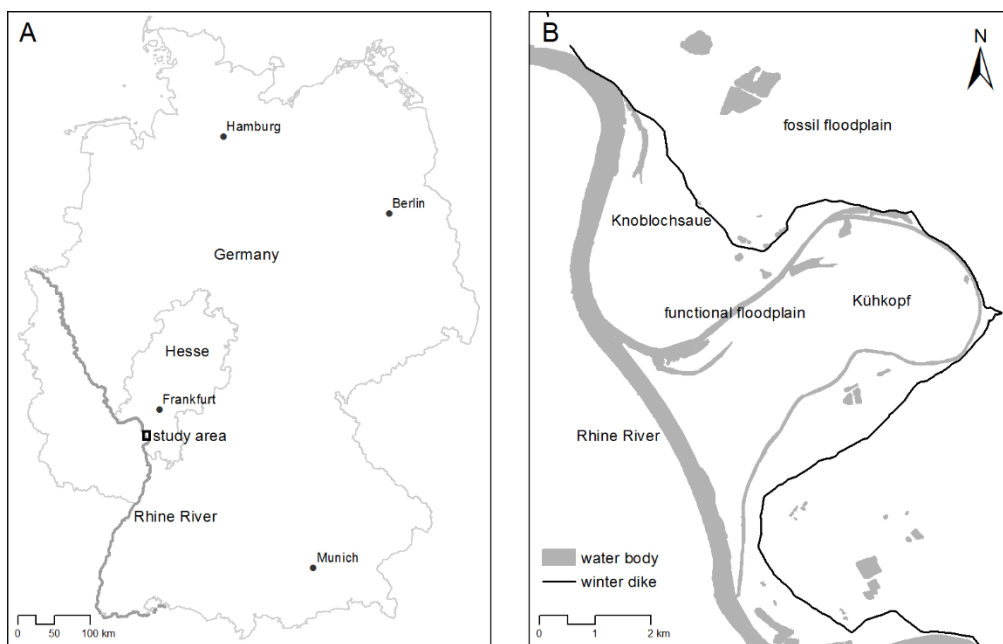
The main objectives of this thesis were to assess the effects of flooding events in floodplain meadow species and to analyze their potential habitats in order to deduce recommendations for restoration practice in regularly flooded grassland habitats.

Specifically, this thesis focused on the following objectives:

1. Analysis of the role of timing of a flooding event in relation to the plant life cycle (i.e., seedling age) and soil composition in flooding tolerance of floodplain meadow species (experimental study; Chapter 2)
2. Evaluation of the interplay between the components flooding depth and duration with respect to flooding tolerance of floodplain meadow species (experimental study; Chapter 3)
3. Investigation of the influence of numerous environmental – in particular hydrological – variables on the distribution of floodplain meadow species and therewith determination of the key variables (habitat modeling; Chapter 4)
4. Habitat-suitability analysis of potential floodplain meadow restoration target sites (habitat modeling; Chapter 4)

## Study area

The study area encompasses the Hessian part of the floodplains along the northern Upper Rhine, which is located approximately 30 km southwest of Frankfurt, Germany (UTM: 32U 453000 5525000–32U 463000 5514000) (Fig. 1.1A). The climatic conditions in this region are relatively warm and dry, with a mean daily temperature of approximately 10.4 °C (1996–2016) and a mean annual precipitation of 725 mm (1996–2016) (Deutscher Wetterdienst DWD, Offenbach, Germany). Fine-grained calcareous alluvial soils, often in combination with sandy sediments of the Rhine, can predominantly be found in the area (Böger 1991). The study area was particularly altered during the straightening of the Rhine River – by the engineer Johann Gottfried Tulla in the 1820s – resulting in the formation of an eastern Rhine island (Kühkopf) bordered by the Rhine and its ancient river bed (Old Rhine) (Fig. 1.1B) (Böger 1991). Furthermore, a winter dike divides the area into a functional floodplain riverwards the dike and a fossil floodplain; the functional floodplain is frequently directly flooded whereas the fossil floodplain is only indirectly submerged in low depressions by ascending groundwater during high water levels of the Rhine River (Hölzel and Otte 2001; Brunotte et al. 2009). The area is characterized by strong seasonal and interannual fluctuations of the Rhine water level (maximum amplitude > 6 m) leading to substantial groundwater table fluctuations (Böger 1991; Bissels et al. 2005).



**Fig. 1.1** Geographic location of the study area in Germany (A), and the study area with its hydrological compartments (functional and fossil floodplain) (B). Data source: © GeoBasis-DE 2018, Federal Agency for Cartography and Geodesy (Bundesamt für Kartographie und Geodäsie, BKG), and Brunotte et al. (2009).

Along the Hessian Upper Rhine, only a small number of old, species-rich meadows still exists. Those meadows were under continuous non-intensive use (i.e., 1–2 times cutting per year, including cut material removal) and have not been converted to arable land, such as the bigger part of the grassland in this region (Böger 1991). Since the 1980s, numerous species-rich floodplain meadows have been reestablished (Donath et al. 2007; Schmiede et al. 2009; Harnisch et al. 2014). This has been achieved through the transfer of freshly cut, seed-containing plant material on former arable land or species-poor grassland sites. Today, the floodplain meadows of this area are among the last and most important strongholds of several rare and endangered floodplain meadow species in Central Europe (Burkart 2001; Mathar et al. 2015). Therefore, this study area at the Hessian Upper Rhine and its grassland species are ideal to investigate the effects of flooding events on floodplain meadow species.

For the experimental part of this thesis (Chapters 2 & 3), defining a study area in the strict sense is not applicable as these common garden experiments focus on plant species commonly occurring in floodplain meadows (EU habitats directive habitat type 6440: alluvial meadows of river valleys of the *Cnidion dubii*). However, sampling of seeds for the second experiment (Chapter 3) was partially performed in floodplain grassland of the Hessian Upper Rhine Valley. Similarly, all vegetation surveys incor-

porated in the habitat modeling (Chapter 4) were conducted in the Hessian Upper Rhine floodplain.

## Chapter outline

This thesis is based on three manuscripts which have all been submitted to international peer-reviewed scientific journals and form the Chapters 2, 3, and 4 of this thesis. Two of the manuscripts have been published (Chapters 2 & 3), and one has been submitted and is currently under peer-review (Chapter 4). The studies in the Chapters 2 & 3 aimed at gaining basic knowledge of flooding tolerance patterns of floodplain meadow species, in order to deduct implications for restoration management. Subsequently, this knowledge served as a basis for the identification of explanatory variables in the study that focuses on the habitat modeling of numerous floodplain meadow species (Chapter 4).

This section gives a brief outline of the contents of the manuscripts and provides an overview of the applied methods. The main findings and conclusions are presented in the subsequent section (Main results and conclusions).

### **Chapter 2** Flooding tolerance of four floodplain meadow species depends on age

This manuscript presents an investigation of the effects of flooding on seedlings of different ages of four typical floodplain meadow plant species. To this end, I flooded seedlings of two familial pairs of species with preference for wetter (*Sanguisorba officinalis* and *Veronica maritima*) and drier microhabitats (*Sanguisorba minor* and *Veronica teucrium*) for 2 weeks each. The flooding procedure started 2, 4, 6, and 8 weeks after seedling germination, respectively. Furthermore, to test for the effect of sand content on the flooding tolerance, I employed two types of soil composition (i.e., soil:sand ratios of 3:1 vs. 1:1) in the flooding experiment. In total, 400 plant individuals were studied in this experiment: 4 plant species  $\times$  5 age groups (4 groups differing in seedling age at start of flooding period, and 1 unflooded control)  $\times$  2 types of soil composition  $\times$  10 replicates. The survival, plant height, leaf number, aboveground biomass, and specific leaf area were assessed. Finally, to examine the effects of seedling age, species, microhabitat preference, and soil composition on survival and performance of plants, I conducted Kaplan-Meier survival analyses, accelerated failure time models, and ANOVAs.

### **Chapter 3** Interaction between depth and duration matters: flooding tolerance of 12 floodplain meadow species

This manuscript presents a study that aims to reveal the effects of flooding duration and flooding depth, as well as their interaction, on seedlings of 12 floodplain meadow plant species. Therefore, I performed flooding procedures for the duration of 2 and 4 weeks with no, partial and complete submergence (i.e., flooding depth). Seedlings of floodplain meadow species in six familial pairs with a preference for relatively wetter or drier microhabitats were utilized for this experiment. Here, I studied a total of 648 experimental plants (12 plant species  $\times$  3 flooding depths  $\times$  2 flooding durations  $\times$  9 replications). The response variables total plant height, root length, above-ground biomass, belowground biomass, total biomass, specific leaf area, and root mass fraction were quantified. To account for the effects of species, microhabitat preference, flooding depth, flooding duration, and their interactions, I conducted multifactorial ANCOVAs for each response variable by including the covariate plant height before the start of the flooding treatment. Subsequently, I computed post hoc Tukey's HSD tests for pairwise comparisons between the treatment groups.

### **Chapter 4** Modeling of rare flood meadow species distribution by a combined habitat-surface water-groundwater model

This manuscript presents a newly developed modeling framework for 23 floodplain meadow plant species, which have been in the focus of floodplain meadow restoration. The framework consists of a combination of a physically-based, surface water-groundwater model, and a habitat model and presents a methodology that has not been tested so far. The surface water-groundwater model represented the hydrological conditions of the floodplain and served as the basis for the hydrological predictors of the habitat model. It was generated using hydrological information from groundwater and river water levels, meteorological data, and a digital elevation model. Apart from the hydrological predictors, also meteorological and morphological predictors were included in the habitat model to simulate the occurrence of the target species. After the identification of the best and most powerful predictors, the best 100 predictor sets (i.e., computed using a standard species distribution model strategy) were used for the calculation of ensembles of small models (i.e., ESM strategy as described by Breiner et al. 2015). To benchmark the new framework, results were compared to a conventional approach with simple hydrological information generated from readily available observation data alone (river water level, groundwater level). Subsequently, several linear mixed-effects models and ANOVAs were calculated to analyze the dif-

ferences in modeling results of these approaches. In addition, the results were compared by grouping the species with respect to their Red List status in Hesse, and the classification as a floodplain meadow species according to Burkart (2001).

## Main results and conclusions

### *Flooding tolerance of floodplain meadow species*

In general, floodplain meadow species are known to be able to withstand the particular conditions to which they are exposed during flooding events (Burkart 2001). Nevertheless, in comparison to several other wetland plants (e.g., reed species, Webb et al. 2012) the floodplain meadow species I studied usually suffer from the detrimental effects of flooded conditions, which results in decreased survival or performance: I showed that a 2-week-flooding treatment had a negative effect on survival and performance of seedlings younger than 6 weeks and that summer floods with high floodwater temperatures may have particular detrimental effects (Chapter 2). Surprisingly, soil composition did not affect plant performance in the experiment (Chapter 2; this issue will be addressed in the next section). Furthermore, I gave evidence that an increased flooding duration and flooding depth, as well as the interactive effect of these two factors negatively affect the performance of plants (Chapter 3).

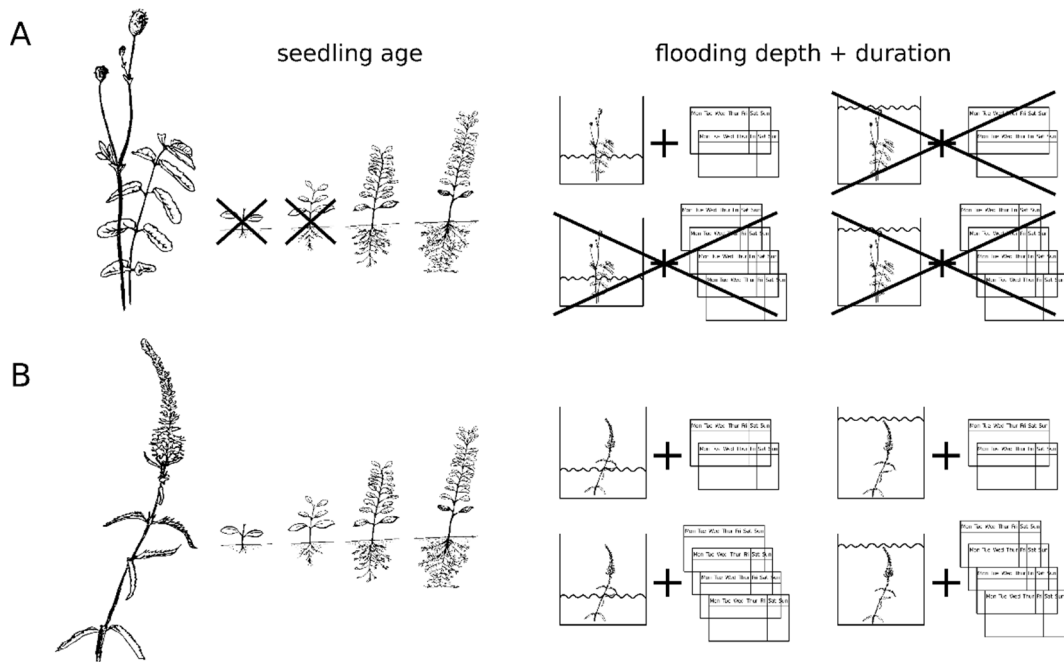
The species' sensitivity to the combination of these two components of a flood seems to play a crucial role in their capacity to establish in riparian grassland. The investigation of interactions of individual factors seems to be underestimated in experimental studies focusing on flooding effects in plants (e.g., Webb et al. 2012). In addition, the results of such studies are often difficult to evaluate or compare if only one key factor (e.g., flooding depth) was taken into account. Hence, interactive effects of flooding components, in particular combinations that include flooding depth and duration, should be studied in more detail to further understand plant responses to flooding events.

In the experiments, several plant performance indicators were diminished with increasing flooding stress (i.e., young plant age, high flooding duration and depth; Chapters 2 & 3). This reduced plant performance is a result of the diminished oxygen and light availability during floods, which leads to limited aerobic respiration and photosynthesis rates (Bailey-Serres and Voesenek 2008). However, several species show phenotypically plastic reactions on the flooding stress by using processes such as underwater photosynthesis or increased shoot elongation for reducing flooding-stress

limitations (Voeselek et al. 2006). These mechanisms represent morphological, metabolic, and anatomical adaptation of plants (Bailey-Serres and Voeselek 2008).

The tested floodplain meadow species are ecologically rather heterogeneous (Burkart 2001) and thus it is not surprising that different species are known to show divergent responses to flooded conditions (Van Eck et al. 2004; Van Eck et al. 2006; Jung et al. 2008). Likewise, I showed that the flooding tolerance regarding several factors was species specific in both experimental studies (Chapters 2 & 3). The different responses of species seem to reflect the various strategies that species pursue to overcome the submergence. Voeselek and Bailey-Serres (2013) conceptualized two opposing strategies, which characterize the extremes on a continuum of survival strategies to flooding. In the “low-oxygen escape syndrome”, triggered by partial submergence, plants try to escape through elongation of aerial organs and thus try to avoid total submergence (Voeselek and Bailey-Serres 2013). Under complete submergence plants show quiescence of metabolism and growth to protect organs, which has been named “low-oxygen quiescence syndrome” (Voeselek and Bailey-Serres 2013). In both experiments, I found evidence for the mentioned strategies; *Veronica maritima* (8 weeks age group, Chapter 2) and *Allium angulosum*, *Silaum silaus*, and *Selinum carvifolia* (partial flooding group, Chapter 3) responded with a slight (though not significant) elongation of shoots, which could be interpreted as an escape strategy. Most of the species with preference to drier microhabitats (e.g., *Veronica teucrium* (Chapter 2), and *Veronica teucrium*, *Sanguisorba minor*, and *Galium wirtgenii* (Chapter 3)) reacted with suppressed elongation, in particular when flooding stress is high (i.e., young age of plants, long flooding duration, high flooding depth), which seems to indicate a quiescence strategy. Interestingly, some plant species are able to switch their strategies depending on flooding depth (Chapter 3; Manzur et al. 2009). Manzur et al. (2009) hypothesize that this ability might define the species’ success in environments with unpredictable floodwater depths. Regarding floodplain meadow species this assumption not only underlines the species’ suitable adaptation to cope with regular flooding, but also could be one common functional trait of floodplain meadow species that has been missing for decades (cf. Burkart 2001). Burkart (2001) concludes that a classification of functional groups of floodplain meadow species would be an essential element to enhance their conservation strategy on a continental scale. To further explore this topic, an experiment with, for instance, fine gradation of flooding depth levels could provide confirmation for this evidence I revealed in my research.

As expected, the species showed flooding tolerance patterns that correspond to their Ellenberg indicator value for moisture (EIV m, Ellenberg et al. 1991) in both



**Fig. 1.2** Flooding tolerance of *Sanguisorba officinalis* (A), and *Veronica maritima* (B) studied in flooding experiments for the factors seedling age (Chapter 2), and flooding depth and duration (Chapter 3). In a first experiment, the effect of seedling age was studied using a 2-week flooding treatment, starting 2, 4, 6, and 8 weeks after seedling germination, respectively. Furthermore, in a second experiment the factors flooding depth (i.e., partial and complete submergence) and duration (2 weeks and 4 weeks) were analyzed. Saint Andrew's crosses indicate factor levels / factor-level combinations that the plants could not tolerate and that led to severe damage.

experiments (Chapters 2 & 3). For *Sanguisorba* and *Veronica* species, which were studied in the two experiments, also a similar pattern in both studies was detected; *Veronica maritima* (EIV m: 8), for instance, is able to cope with submergence even with young age and can withstand floods with a duration of 4 weeks under complete submergence relatively well. By contrast, *Sanguisorba officinalis* (EIV m: 7) has problems to survive a flood before the age of 6 weeks after germination and struggles when a flooding event continues for longer than 2 weeks and with complete submergence (Fig. 1.2; Chapters 2 & 3). Also Brotherton and Joyce (2015) noted that EIV m seem to be a very meaningful indicator to classify and rank species of wet grasslands.

Overall, the microhabitat preference of species proved to have a strong effect on flooding tolerance patterns of species (Chapters 2 & 3). Likewise, numerous studies have shown the important role of species' preference towards wetter or drier locations with respect to their flooding tolerance and, correspondingly, their differences in the



distribution on a microscale (Vervuren et al. 2003; Van Eck et al. 2004; Lenssen and De Kroon 2005; Van Eck et al. 2006; Jung et al. 2008). Flood tolerant species inherit a number of specific traits in order to overcome flooding (e.g., aerenchyma production, leaf and root anatomy, plant height, and starch storage Voesenek and Bailey-Serres 2015). Especially, root anatomy differs substantially with regard to the species' microhabitat preference; for example, *Sanguisorba officinalis* has relatively short roots (~50–100 cm) with unusually wide secondary phloem (i.e., where nutrients are transported from the shoots towards roots), high amounts of starch storage, and is equipped with aerenchyma tissue in the endodermis (Kutschera and Lichtenegger 1992; Hegi 1995). On the other hand, *Sanguisorba minor* is characterized by long roots (~150 cm) with a thin secondary phloem and a thick cork layer (i.e., protection against drying out). These traits enable *Sanguisorba officinalis* to easily tolerate flooded conditions whereas *Sanguisorba minor* is drought resistant (Kutschera and Lichtenegger 1992). Regarding flooding tolerance, Wright et al. (2017) observed increased plant performance and recovery after a flooding event with increased root aerenchyma content. Aerenchyma tissue enables gas exchange and thus could sustain fundamental plant functioning throughout the flooding event (Visser et al. 2000). In terms of drought resistance, several studies revealed that also the specific adaptations of floodplain meadow species towards limited water availability differ strongly with respect to their microhabitat preference (Ludewig et al. 2014b; Ludewig et al. 2018).

The observed microhabitat gradient from flood tolerance to drought resistance was furthermore described as hydrological niche segregation by Silvertown et al. (2015). It is not only observable in riparian grassland (Silvertown et al. 1999) but also in a number of other ecosystems, such as steppes, deserts, and tropical forests (Silvertown et al. 2015). However, as the hydrological niches seem to define species distribution in floodplain grassland they should be taken into account when planning restoration at these sites.

#### *Modeling species distribution of floodplain meadow species*

Several studies focused on the modeling of plant species distribution in floodplain habitats, although only few studies have modeled floodplain species on a local scale (Leyer 2005; Büchele et al. 2006; Mosner et al. 2011; Mosner et al. 2015). In Chapter 4, I present such a habitat model for 23 riparian species. I showed that model performance differed substantially across these species. Red List species as well as typical floodplain meadow species according to Burkart (2001) showed mostly better modeling performance than other species. Furthermore, different species required a different set of predictor variables in their best modeling runs. Apart from several

hydrological predictors also the meteorological and morphological predictors were among the most frequently utilized predictors. Even the least common predictor (PH15; Table 4.2) contributed to about 10% of the habitat models. In general, including hydrological predictors significantly improved model quality of the habitat model.

Since the hydrological niche segregation plays a crucial role in riparian ecosystems (Silvertown et al. 2015), it is clear that such models should incorporate hydrological information. Hitherto, only simple hydrological predictors (e.g., average water level, average high water level, average standard deviation) from groundwater or river water level gauges have been included in such models (e.g., Leyer 2005; Mosner et al. 2015). Vervuren et al. (2003) pointed out that basic hydrological parameters are not sufficient to incorporate extreme flooding events in the analysis of species distributions. The study in Chapter 4 presents a habitat modeling, which includes several specific hydrological predictor variables that describe, e.g., extreme discharge events (predictors PH10 and PH11; Table 4.2) but also drought periods (predictors PH03–PH05, PH12–PH14; Table 4.2). Furthermore, the calculation of numerous predictors was based on autecological information gained in experiments (Chapters 2 & 3); for instance, the predictor PH10 describes the sum of days on which the inundation height was a minimum 50 cm, which corresponds to the tested interaction of factors flooding duration and depth in the study in Chapter 3. To define variables based on experiments is a beneficial method in the preselection of predictors for habitat models (Guisan et al. 2017). Indeed, several predictors from the final set of 19 predictors (Table 4.2) are linked with the results of the experiments, which confirms the crucial role of the tested effects and might also validate the results.

An interesting outcome of the study in Chapter 4 was regarding the comparison of different databases for the calculation of the hydrological predictors. Apart from the high resolution, coupled surface water-groundwater model (Maier et al. 2017) I also used databases for groundwater and river water level as a basis to calculate the hydrological predictors for the habitat model. The results show that over all species, for rare and endangered species, and for species that are on the list of floodplain meadow species according to Burkart (2001) the predictors derived from the surface water-groundwater model significantly outperform other databases (Chapter 4). So far, only few studies used groundwater or river water data to model riparian species (Leyer 2005; Büchele et al. 2006; Mosner et al. 2011; Mosner et al. 2015). A floodplain habitat model that based on a surface water-groundwater model has not been published so far. This new approach describes the complexity of habitat requirements of the particular group of floodplain meadow species better than interpolated, measured hydrological data. Despite the increased computational effort of the spatially

explicit hydrological modeling (Maier et al. 2017), the new method provides improved model quality. Furthermore, therewith it is possible to calculate scenarios by incorporating data based on land-use or climate change projections (e.g., Volk et al. 2018; Maier et al. 2018).

Riparian habitat models at a regional or continental scale often include other parameters to incorporate the hydrological situation, e.g., topographic wetland index or solely climate variables (Besnard et al. 2013; Ikeda et al. 2014; Fink et al. 2017). In the modeling presented in Chapter 4, I also calculated models including the topographic wetland index in a first modeling step. However, this predictor showed weak explanatory power and thus was removed from the subsequent modeling procedure. In general, habitat models incorporate large scale climate variables such as the WorldClim data (Hijmans et al. 2005) or topographic variables to model species' niches at ecoregional, continental or global scales (Guisan et al. 2017). When modeling at the local level, such variables might not sufficiently describe the species niches (Seo et al. 2009). Likewise, Besnard et al. (2013) showed that models based on the topographic wetland index lead to better goodness of model fit at coarse resolution (250 m pixel size) compared to fine resolution (50 m pixel size). Consequently, predictors such as the topographic wetland index are useful in models at ecoregional scale or higher but should be avoided when modeling with a high spatial resolution.

Although, in general, the soil composition strongly affects vegetation composition (Ellenberg 2009; Blume et al. 2016), the results from the habitat modeling suggest that soil composition only marginally influences plant distribution of floodplain meadow species; the predictor soil type was excluded in the first modeling step due to very low explanatory power for all species (Nagelkerke's  $R^2 < 0.12$ , Chapter 4). Similarly, in the experiment presented in Chapter 2, differing soil composition (i.e., sand content) did not affect plant survival or performance under flooded conditions. Even though these experimental findings cannot be directly transferred to the field (Poorter et al. 2016), they are in line with previous findings that mainly hydrological parameters define plant zonation in riparian ecosystems whereas soil parameters play a subordinate role in this respect (Castelli et al. 2000; Leyer 2006). The interplay of the soil moisture content and soil particle size seems to be intercorrelated with hydrological parameters (Castelli et al. 2000). Hence, these aspects might be better integrated in habitat modeling through hydrological predictors than by using soil maps, which are often generated on a too coarse resolution (Guisan and Zimmermann 2000).

Only few studies have tested the applicability of the “ensembles of small models” approach for rare species modeling (Breiner et al. 2015; Di Febbraro et al. 2017;

Breiner et al. 2018). I provide a habitat model for 23 riparian species, which represents another application example for this method (Chapter 4). In conclusion, this method seems to be a feasible approach to model rare and endangered target species of restoration projects. The enlarged transferability and model performance are highly advantageous compared to standard habitat models of rare species, even though computation time is increased (Breiner et al. 2018). Therefore, I can encourage scientists as well as practitioners to compute models for restoration purposes using this method.

#### *Implications for restoration management and perspectives*

From a restoration ecological perspective, the results of this thesis suggest that flooding during the vegetation period might act as an obstacle for restoration management on floodplain meadows; particularly, the reestablishment of rare plant species (e.g., via the transfer of seed-containing plant material) is susceptible to floods as favorable outcome of those measures depends on successful seedling establishment in the year after the measure (Kiehl et al. 2010). In general, microsite conditions – including hydrological – play a crucial role in the restoration of floodplain grassland (Donath et al. 2007; Engst et al. 2016). Consequently, the impact of flooding on the establishment of restoration target species – and thus restoration success – should be considered.

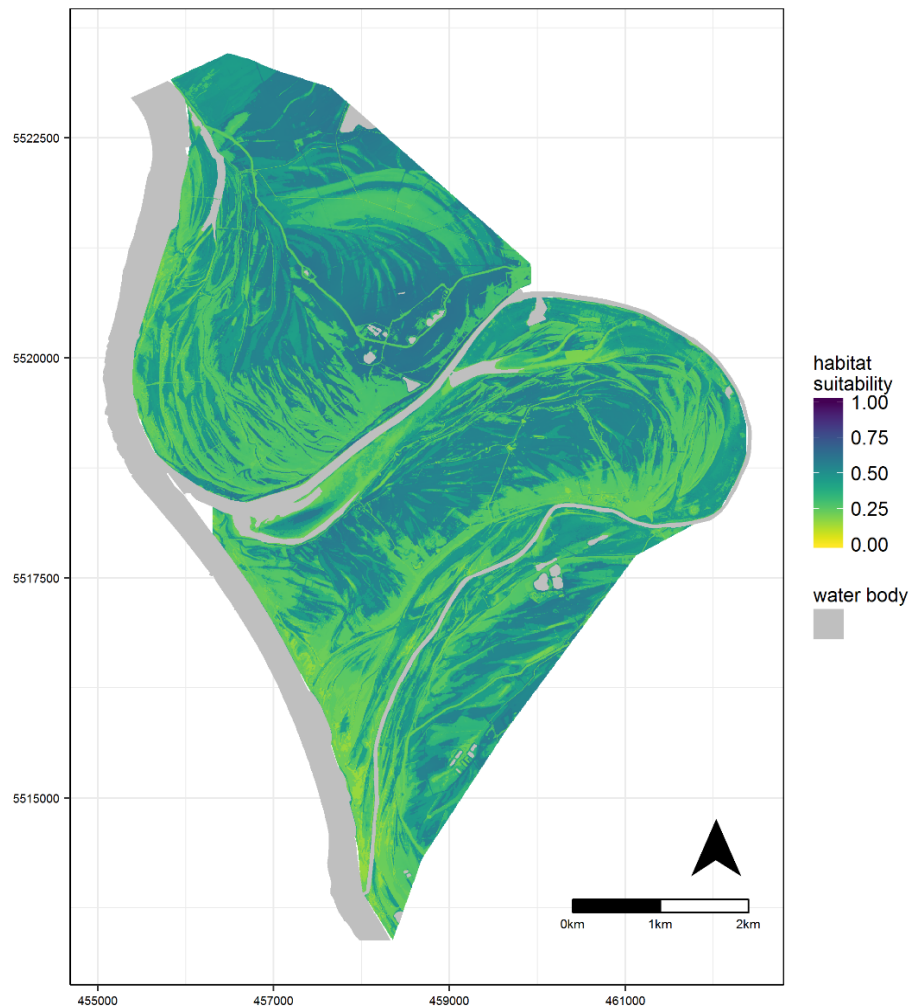
In both experiments, hints for the existence of tipping points could be detected; floodplain meadow plants are more likely to survive a flooding event, if (1) they are older than about 6 weeks after germination (Chapter 2), and if (2) the combination of flooding duration and depth is below a species specific level (Chapter 3). In this thesis, I present the first published study (Chapter 3) that recognized tipping points with regard to extreme climate events (i.e., flooding events) in riparian grassland, which also Brotherton and Joyce (2015) identified as urgently necessary to investigate. The knowledge of the tipping points of species in focus of conservationists could facilitate conservation management, especially on sites with ecological (i.e., managed) flooding (e.g., Cyffka et al. 2016). The schedule of gate openings on those sites could be adjusted in order to avoid exceeding the tipping point conditions in the year after restoration measures. That would improve the recruitment of target species as well as the restoration outcome. Consequently, tipping points in floodplain meadow species should be studied in further detail.

Although flooding might raise difficulties for restoration management during planning and realization of restoration measures, regular flooding plays a vital role for the persistence of the particular floodplain meadow species in their habitat. There-

fore, habitat-suitability maps are an ideal tool in order to determine sites with environmental conditions (i.e., flooding duration, depth, frequency, etc.) that match with the habitat requirements of the target species (Guisan et al. 2013). I generated such habitat-suitability maps based on the habitat model presented in Chapter 4 for floodplain meadow plants in the study area (Fig. 1.3). For future restoration projects, these habitat-suitability maps could serve as a tool to select restoration sites and thus facilitate the restoration management. Furthermore, a well-directed selection of target sites enables saving economic and other restricted resources (e.g., freshly-mown, seed-containing plant material) through a reduction of false investments (i.e., restoration on unsuitable locations).

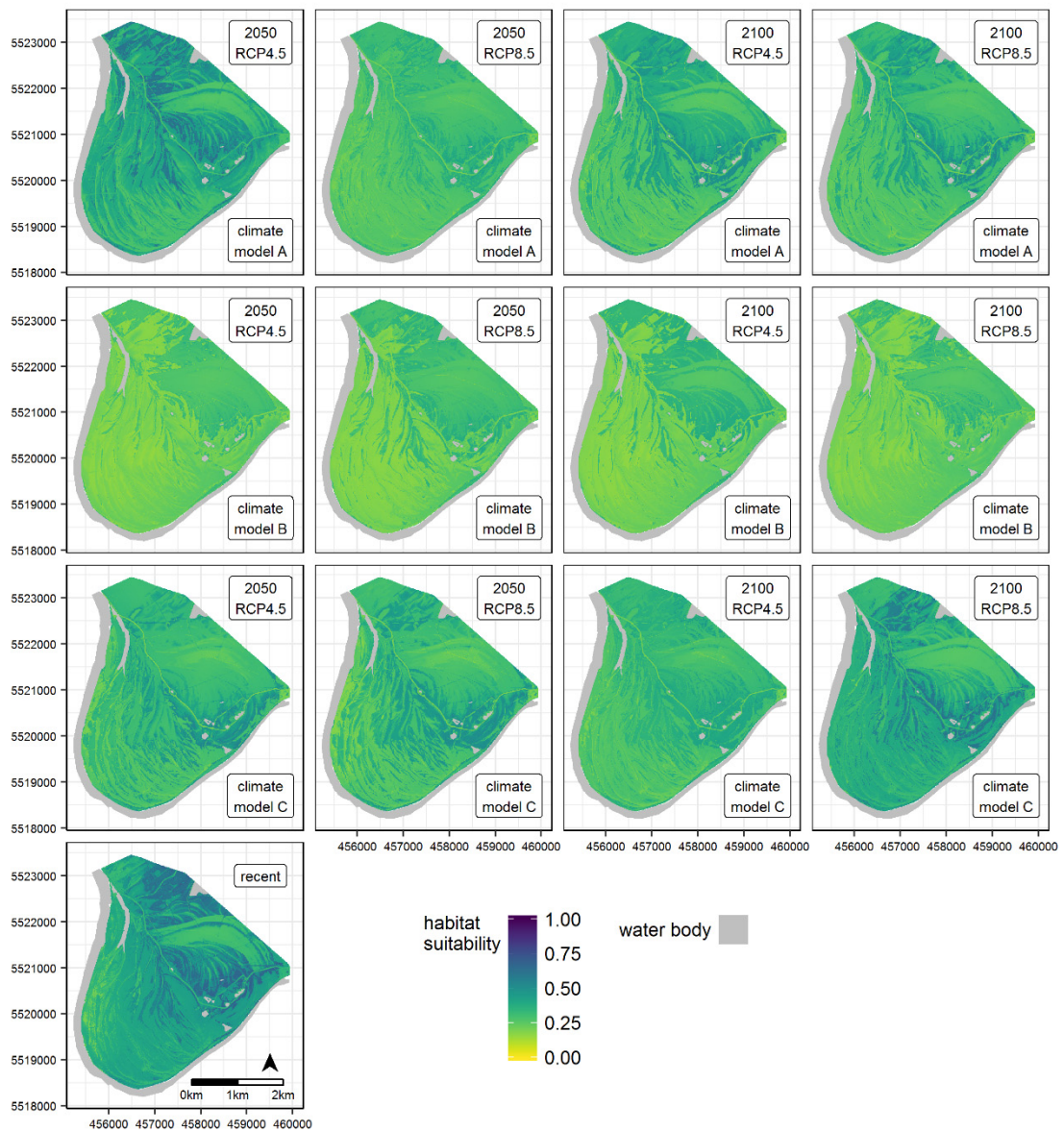
When using habitat models in restoration planning, it is crucial that modelers and conservationists are working closely together and that as a result, model and decision process are tightly interwoven (Guisan et al. 2013). Hence, the integration of the intrinsic knowledge of stakeholders of floodplain meadow restoration (e.g., conservation practitioners, nature conservation authorities) as well as the autecological characteristics of the target species (e.g., the experimentally studied flooding tolerance of the target species; Chapters 2 & 3) seems to be essential in the modeling of floodplain meadow species. For this reason, data and knowledge of local management authorities and colleagues from the Division of Landscape Ecology and Planning – who have been restoring floodplain grassland since more than 20 years – were included in the modeling (Chapter 4). Therefore, the generated habitat maps (Fig. 1.3) should be able to serve as a solid baseline in the selection of target sites for upcoming restoration projects.

For the enhancement of long-term restoration success, it might not be sufficient to solely focus on habitat suitability when selecting target sites. In a recent study, colleagues and I developed a new, easily applicable methodology to estimate restoration success through connectivity analysis (Volk et al. 2018). We showed that small isolated populations of target species have an increased risk of extinction and therefore the development of larger populations with high connectivity should be in focus of restoration planning (Volk et al. 2018). By combining the habitat model (Chapter 4) with a connectivity analysis of already populated habitats, sites with low connectivity but high habitat suitability could be detected. On these locations, colonization initials of the target species should be reestablished to increase the chance for establishing viable, self-sustaining populations. This approach could further strengthen the decision-making process in restoration planning.



**Fig. 1.3** Exemplary map of habitat suitability for the floodplain meadow species *Sanguisorba officinalis* in the study area. Based on the habitat model presented in Chapter 4, projections of the habitat suitability of species can be generated. Consequently, target sites for floodplain meadow restoration projects – with a high habitat suitability and thus increased restoration success – can be identified.

In the face of global change, it could be advantageous to examine the habitat suitability of the species based on future environmental conditions. Using the well-calibrated habitat model (Chapter 4) I generated habitat-suitability maps for projected future (hydrological) conditions (Fig. 1.4). The maps are based on modified data from Maier et al. (2018), which also incorporate several climate models and concentration pathways. Therewith, despite the high uncertainty of the underlying climate models (Bosshard et al. 2013), sites with a high probability of suitability in the future could be detected. (e.g., where several climate models project high habitat suitability).



**Fig. 1.4** Exemplary map of habitat suitability of *Sanguisorba officinalis* for projected future (2050, 2100), and recent conditions in the northern part of the study area (Knoblochsaue). Results are shown for two representative concentration pathways (RCP4.5, RCP8.5) and three climate models (A: ICHEC-EC-EARTH-RACMO22E, B: MOHC-HadGEM2-ES-CCLM4-8-17, C: CNRM-CERFACS-CNRM-CM5-CCLM4-8-17). The maps were generated based on modified data from Maier et al. (2018) using the habitat model from Chapter 4.

The expected substantial changes in altered discharge regimes of large rivers (Middelkoop et al. 2001; Gorgen et al. 2010) are supposed to threaten plant species diversity in Europe (Thuiller et al. 2005). Hence, it might be reasonable to incorpo-

rate these alterations in upcoming restoration measures using maps, such as presented in Figure 1.4.

As shown in this thesis, the predicted pronounced changes in environmental conditions (e.g., increase in flooding intensity; Sperna Weiland et al. 2012) will strongly affect seedling establishment and the outcome of restoration campaigns. Planning of restoration projects on species-rich floodplain meadows will become increasingly difficult but necessary more than ever: Wright et al. (2015; 2017) reported that maintaining high species diversity could buffer against ecosystem function losses due to flooding events in grassland ecosystems.

## References

- Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J Appl Ecol* 43:1223–1232. doi: 10.1111/j.1365-2664.2006.01214.x
- Bailey-Serres J, Voisenek LACJ (2008) Flooding Stress: Acclimations and Genetic Diversity. *Annu Rev Plant Biol* 59:313–339. doi: 10.1146/annurev.arplant.59.032607.092752
- Besnard AG, La Jeunesse I, Pays O, Secondi J (2013) Topographic wetness index predicts the occurrence of bird species in floodplains. *Divers Distrib* 19:955–963. doi: 10.1111/ddi.12047
- Bissels S, Donath TW, Hölzel N, Otte A (2005) Ephemeral wetland vegetation in irregularly flooded arable fields along the northern Upper Rhine: the importance of persistent seedbanks. *Phytocoenologia* 469–488. doi: 10.1127/0340-269X/2005/0035-0469
- Bissels S, Hölzel N, Donath TW, Otte A (2004) Evaluation of restoration success in alluvial grasslands under contrasting flooding regimes. *Biol Conserv* 118:641–650. doi: 10.1016/j.biocon.2003.10.013
- Blom CWPM, Voisenek LACJ, Banga M, Engelaar WMHG, Rijnders JHGM, Van De Steeg HM, Visser EJW (1994) Physiological Ecology of Riverside Species: Adaptive Responses of Plants to Submergence. *Ann Bot* 74:253–263. doi: 10.1006/anbo.1994.1116
- Blume H-P, Brümmer GW, Fleige H, Horn R, Kandeler E, Kögel-Knabner I, Kretschmar R, Stahr K, Wilke B-M (2016) Scheffer/Schachtschabel Soil Science, 1st edn. Springer, Berlin Heidelberg
- Böger K (1991) Grünlandvegetation im Hessischen Ried. Pflanzensoziologische Verhältnisse und Naturschutzkonzeption (Grassland vegetation in the Hessian Ried. Plant sociology and nature conservation concept). Botanische Vereinigung für Naturschutz in Hessen (BVNH), Frankfurt/Main



- Bosshard T, Kotlarski S, Zappa M, Schär C (2013) Hydrological Climate-Impact Projections for the Rhine River: GCM–RCM Uncertainty and Separate Temperature and Precipitation Effects. *J Hydrometeorol* 15:697–713. doi: 10.1175/JHM-D-12-098.1
- Breiner FT, Guisan A, Bergamini A, Nobis MP (2015) Overcoming limitations of modelling rare species by using ensembles of small models. *Methods Ecol Evol* 6:1210–1218. doi: 10.1111/2041-210X.12403
- Breiner FT, Nobis MP, Bergamini A, Guisan A (2018) Optimizing ensembles of small models for predicting the distribution of species with few occurrences. *Methods Ecol Evol* 9:802–808. doi: 10.1111/2041-210X.12957
- Brotherton SJ, Joyce CB (2015) Extreme climate events and wet grasslands: plant traits for ecological resilience. *Hydrobiologia* 750:229–243. doi: 10.1007/s10750-014-2129-5
- Brunotte E, Dister E, Günther-Diringer D, Koenzen U, Mehl D (2009) Flussauen in Deutschland. Erfassung und Bewertung des Auenzustandes (Floodplains in Germany. Recording and evaluation of floodplain conditions). *Naturschutz Biol Vielfalt* 87:1–141
- Büchle B, Burek P, Baufeld R, Leyer I (2006) Modelling flood plain vegetation based on long-term simulations of daily river–groundwater dynamics. *Predict Ungauged Basins Promise Prog Proc Symp S7 Held Seventh IAHS Sci Assem Foz Iguaçu Braz April 2005* 318–333
- Bunn SE, Arthington AH (2002) Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity. *Environ Manage* 30:492–507. doi: 10.1007/s00267-002-2737-0
- Burkart M (2001) River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. *Glob Ecol Biogeogr* 10:449–468. doi: 10.1046/j.1466-822x.2001.00270.x
- Burkart M, Dierschke H, Hölzel N, Nowak B, Fartmann T (2004) Molinio-Arrhenatheretea (E1) - Kulturgrasland und verwandte Vegetationstypen (Molinio-Arrhenatheretea E1 - Cultural grassland and related vegetation types). *Synop Pflanzengesellschaften Dtschl* 1–103
- Burmeier S, Eckstein RL, Otte A, Donath TW (2010) Desiccation cracks act as natural seed traps in flood-meadow systems. *Plant Soil* 333:351–364. doi: 10.1007/s11104-010-0350-1
- Burmeier S, Eckstein RL, Otte A, Donath TW (2011) Spatially-restricted plant material application creates colonization initials for flood-meadow restoration. *Biol Conserv* 144:212–219. doi: 10.1016/j.biocon.2010.08.018
- Castelli RM, Chambers JC, Tausch RJ (2000) Soil-plant relations along a soil-water gradient in great basin riparian meadows. *Wetlands* 20:251–266. doi: 10.1672/0277-5212(2000)020[0251:SPRAAS]2.0.CO;2
- Cronk JK, Fennessy MS (2001) *Wetland Plants: Biology and Ecology*. CRC Press, Boca Raton, FL
- Cyffka B, Binder F, Ewald J, Geist J, Gruppe A, Hemmer I, Kiehl K, Mosandl R, Schopf R, Zahner V (2016) Neue dynamische Prozesse im Auenwald. Monitoring der Auenrenaturierung an der Donau zwischen Neuburg und Ingolstadt (New dynamic processes in the floodplain forest.

- Monitoring of the floodplain restoration along the Danube between Neuburg and Ingolstadt). *Naturschutz Biol Vielfalt* 150:1–379
- Di Febbraro M, Carotenuto F, Castiglione S, Russo D, Loy A, Maiorano L, Raia P (2017) Does the jack of all trades fare best? Survival and niche width in Late Pleistocene megafauna. *J Biogeogr* 44:2828–2838. doi: 10.1111/jbi.13078
- Donath TW, Bissels S, Hölzel N, Otte A (2007) Large scale application of diaspore transfer with plant material in restoration practice – Impact of seed and microsite limitation. *Biol Conserv* 138:224–234. doi: 10.1016/j.biocon.2007.04.020
- Donath TW, Hölzel N, Otte A (2003) The impact of site conditions and seed dispersal on restoration success in alluvial meadows. *Appl Veg Sci* 6:13–22. doi: 10.1111/j.1654-109X.2003.tb00560.x
- Elith J, Leathwick JR (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annu Rev Ecol Evol Syst* 40:677–697. doi: 10.1146/annurev.ecolsys.110308.120159
- Ellenberg H (2009) *Vegetation Ecology of Central Europe*, 4th edn. Cambridge University Press, Cambridge, New York
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1991) *Zeigerwerte von Pflanzen in Mitteleuropa (Indicator values of plants in Central Europe)*, 3rd edn. Goltze, Göttingen
- Engst K, Baasch A, Erfmeier A, Jandt U, May K, Schmiede R, Bruehlheide H (2016) Functional community ecology meets restoration ecology: Assessing the restoration success of alluvial floodplain meadows with functional traits. *J Appl Ecol* 53:751–764. doi: 10.1111/1365-2664.12623
- Finck P, Heinze S, Rath U, Riecken U, Szymank A (2017) Rote Liste der gefährdeten Biotoptypen Deutschlands. Dritte fortgeschriebene Fassung (Red list of threatened habitat types in Germany. Third updated version). *Naturschutz Biol Vielfalt* 156:1–460
- Fink S, Lanz T, Stecher R, Scheidegger C (2017) Colonization potential of an endangered riparian shrub species. *Biodivers Conserv* 26:2099–2114. doi: 10.1007/s10531-017-1347-3
- Geissler K, Gzik A (2008) The impact of flooding and drought on seeds of *Cnidium dubium*, *Gratiola officinalis*, and *Juncus atratus*, three endangered perennial river corridor plants of Central European lowlands. *Aquat Bot* 89:283–291. doi: 10.1016/j.aquabot.2008.03.001
- Gilgen AK, Buchmann N (2009) Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. *Biogeosciences* 6:2525–2539. doi: 10.5194/bg-6-2525-2009
- Giller PS, Malmqvist B (1998) *The Biology of Streams and Rivers*. Oxford University Press, Oxford
- Görgen K, Beersma J, Brahmer G, Buiteveld H, Carambia M, de Keizer O, Krahe P, Nilson E, Lammersen R, Perrin C, Volken D (2010) Assessment of climate change impacts on discharge in the Rhine River Basin: results of the RheinBlick2050 project. CHR, Lelystad

- Greet J, Angus Webb J, Cousens RD (2011) The importance of seasonal flow timing for riparian vegetation dynamics: a systematic review using causal criteria analysis: Effects of seasonal flow timing on riparian flora. *Freshw Biol* 56:1231–1247. doi: 10.1111/j.1365-2427.2011.02564.x
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009. doi: 10.1111/j.1461-0248.2005.00792.x
- Guisan A, Thuiller W, Zimmermann NE (2017) *Habitat Suitability and Distribution Models: With Applications in R*. Cambridge University Press
- Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. *Ecol Lett* 16:1424–1435. doi: 10.1111/ele.12189
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Model* 135:147–186. doi: 10.1016/S0304-3800(00)00354-9
- Hanke JM, Ludewig K, Jensen K (2014) Effects of water level and competition on the endangered river corridor plant *Cnidium dubium* in the context of climate change. *Wetl Ecol Manag* 1–12. doi: 10.1007/s11273-014-9371-5
- Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 143:29–36. doi: 10.1148/radiology.143.1.7063747
- Harnisch M, Otte A, Schmiede R, Donath TW (2014) Verwendung von Mahdgut zur Renaturierung von Auengrünland (Use of seed-containing plant material for the restoration of floodplain grassland). Eugen Ulmer, Stuttgart
- Hegi G (1995) *Illustrierte Flora von Mitteleuropa, Band IV, Teil 2B (Illustrated Flora of Central Europe, Volume IV, Part 2B)*, 2nd edn. Blackwell Wissenschafts-Verlag, Berlin
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978. doi: 10.1002/joc.1276
- Hölzel N, Otte A (2004) Inter-annual variation in the soil seed bank of flood-meadows over two years with different flooding patterns. *Plant Ecol* 174:279–291. doi: 10.1023/B:VEGE.0000049108.04955.e2
- Hölzel N, Otte A (2001) The impact of flooding regime on the soil seed bank of flood-meadows. *J Veg Sci* 12:209–218. doi: 10.2307/3236605
- Ikeda DH, Grady KC, Shuster SM, Whitham TG (2014) Incorporating Climate Change and Exotic Species into Forecasts of Riparian Forest Distribution. *PLoS ONE* 9:e107037. doi: 10.1371/journal.pone.0107037
- Joyce CB, Wade PM (1998) Wet Grasslands: A European Perspective. In: Joyce CB, Wade PM (eds) *European Wet Grasslands: Biodiversity, Management and Restoration*. Wiley, Chichester, UK, pp 1–12

- Jung V, Hoffmann L, Muller S (2008) Ecophysiological responses of nine floodplain meadow species to changing hydrological conditions. *Plant Ecol* 201:589–598. doi: 10.1007/s11258-008-9508-9
- Kiehl K, Kirmer A, Donath TW, Rasran L, Hölzel N (2010) Species introduction in restoration projects – Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic Appl Ecol* 11:285–299. doi: 10.1016/j.baae.2009.12.004
- Kutschera L, Lichtenegger E (1992) *Wurzelatlas mitteleuropäischer Grünlandpflanzen (Root Atlas of Central European Grassland Plants)*. Gustav Fischer Verlag, Stuttgart
- Lenssen JPM, De Kroon H (2005) Abiotic constraints at the upper boundaries of two *Rumex* species on a freshwater flooding gradient. *J Ecol* 93:138–147. doi: 10.1111/j.1365-2745.2004.00957.x
- Leyer I (2005) Predicting plant species' responses to river regulation: the role of water level fluctuations. *J Appl Ecol* 42:239–250. doi: 10.1111/j.1365-2664.2005.01009.x
- Leyer I (2006) Dispersal, diversity and distribution patterns in pioneer vegetation: The role of river-floodplain connectivity. *J Veg Sci* 17:407–416. doi: 10.1111/j.1654-1103.2006.tb02461.x
- Lomba A, Pellissier L, Randin C, Vicente J, Moreira F, Honrado J, Guisan A (2010) Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. *Biol Conserv* 143:2647–2657. doi: 10.1016/j.biocon.2010.07.007
- Ludewig K, Hanke JM, Wuthe B, Otte A, Mosner E, Eckstein RL, Donath TW (2018) Differential effect of drought regimes on the seedling performance of six floodplain grassland species. *Plant Biol* 20:691–697. doi: 10.1111/plb.12722
- Ludewig K, Korell L, Löffler F, Scholz M, Mosner E, Jensen K (2014a) Vegetation patterns of floodplain meadows along the climatic gradient at the Middle Elbe River. *Flora - Morphol Distrib Funct Ecol Plants* 209:446–455. doi: 10.1016/j.flora.2014.04.006
- Ludewig K, Zelle B, Eckstein RL, Mosner E, Otte A, Donath TW (2014b) Differential effects of reduced water potential on the germination of floodplain grassland species indicative of wet and dry habitats. *Seed Sci Res* 24:49–61. doi: 10.1017/S096025851300038X
- Madsen TV, Sand-Jensen K (1994) The interactive effects of light and inorganic carbon on aquatic plant growth. *Plant Cell Environ* 17:955–962. doi: 10.1111/j.1365-3040.1994.tb00324.x
- Magee TK, Kentula ME (2005) Response of wetland plant species to hydrologic conditions. *Wetl Ecol Manag* 13:163–181. doi: 10.1007/s11273-004-6258-x
- Maier N, Breuer L, Chamorro A, Kraft P, Houska T (2018) Multi-Source Uncertainty Analysis in Simulating Floodplain Inundation under Climate Change. *Water* 10:809. doi: 10.3390/w10060809
- Maier N, Breuer L, Kraft P (2017) Prediction and uncertainty analysis of a parsimonious floodplain surface water-groundwater interaction model. *Water Resour Res* 53:7678–7695. doi: 10.1002/2017WR020749
- Malanson GP (1993) *Riparian Landscapes*. Cambridge University Press, Cambridge

- Manzur ME, Grimoldi AA, Insausti P, Striker GG (2009) Escape from water or remain quiescent? *Lotus tenuis* changes its strategy depending on depth of submergence. *Ann Bot* 104:1163–1169. doi: 10.1093/aob/mcp203
- Mathar W, Kleinebecker T, Hölzel N (2015) Environmental variation as a key process of co-existence in flood-meadows. *J Veg Sci* 26:480–491. doi: 10.1111/jvs.12254
- Mauchamp A, Blanch S, Grillas P (2001) Effects of submergence on the growth of *Phragmites australis* seedlings. *Aquat Bot* 69:147–164. doi: 10.1016/S0304-3770(01)00135-8
- Middelkoop H, Daamen K, Gellens D, Grabs W, Kwadijk JC, Lang H, Parment BW, Schädler B, Schulla J, Wilke K (2001) Impact of climate change on hydrological regimes and water resources management in the Rhine basin. *Clim Change* 49:105–128. doi: 10.1023/A:1010784727448
- Mosner E, Schneider S, Lehmann B, Leyer I (2011) Hydrological prerequisites for optimum habitats of riparian *Salix* communities - identifying suitable reforestation sites: Optimum habitats of riparian *Salix* communities. *Appl Veg Sci* 14:367–377. doi: 10.1111/j.1654-109X.2011.01121.x
- Mosner E, Weber A, Carambia M, Nilson E, Schmitz U, Zelle B, Donath T, Horschler P (2015) Climate change and floodplain vegetation—future prospects for riparian habitat availability along the Rhine River. *Ecol Eng* 82:493–511. doi: 10.1016/j.ecoleng.2015.05.013
- 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 Phytol* 144:313–321. doi: 10.1046/j.1469-8137.1999.00519.x
- Naiman RJ, Decamps H, Pollock M (1993) The Role of Riparian Corridors in Maintaining Regional Biodiversity. *Ecol Appl* 3:209–212. doi: 10.2307/1941822
- Peterson AT, Soberón J, Pearson RG, Anderson R, Martinez-Meyer E, Nakamura M, Araújo MB (2011) *Ecological Niches and Geographic Distributions*. Princeton University Press
- Poorter H, Fiorani F, Pieruschka R, Wojciechowski T, Van der Putten WH, Kleyer M, Schurr U, Postma J (2016) Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. *New Phytol* 212:838–855. doi: 10.1111/nph.14243
- Schmiede R, Donath TW, Otte A (2009) Seed bank development after the restoration of alluvial grassland via transfer of seed-containing plant material. *Biol Conserv* 142:404–413. doi: 10.1016/j.biocon.2008.11.001
- Seo C, Thorne JH, Hannah L, Thuiller W (2009) Scale effects in species distribution models: implications for conservation planning under climate change. *Biol Lett* 5:39–43. doi: 10.1098/rsbl.2008.0476
- Shcheglovitova M, Anderson RP (2013) Estimating optimal complexity for ecological niche models: A jackknife approach for species with small sample sizes. *Ecol Model* 269:9–17. doi: 10.1016/j.ecolmodel.2013.08.011

- Silvertown J, Araya Y, Gowing D (2015) Hydrological niches in terrestrial plant communities: a review. *J Ecol* 103:93–108. doi: 10.1111/1365-2745.12332
- Silvertown J, Dodd ME, Gowing DJG, Mountford JO (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* 400:61–63. doi: 10.1038/21877
- Sperna Weiland FC, Van Beek LPH, Kwadijk JCJ, Bierkens MFP (2012) Global patterns of change in discharge regimes for 2100. *Hydrol Earth Syst Sci* 16:1047–1062. doi: 10.5194/hess-16-1047-2012
- Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci U S A* 102:8245–8250. doi: 10.1073/pnas.0409902102
- Tockner K, Stanford JA (2002) Riverine flood plains: present state and future trends. *Environ Conserv* 29:308–330. doi: 10.1017/S037689290200022X
- Van Eck WHJM, Lenssen JPM, Rengeling RHJ, Blom CWPM, De Kroon H (2005) Water temperature instead of acclimation stage and oxygen concentration determines responses to winter floods. *Aquat Bot* 81:253–264. doi: 10.1016/j.aquabot.2004.10.006
- Van Eck WHJM, Lenssen JPM, Van De Steeg HM, Blom CWPM, 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. doi: 10.1007/s10750-005-1905-7
- Van Eck WHJM, Van De Steeg HM, Blom CWPM, 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. doi: 10.1111/j.0030-1299.2004.13083.x
- Vaughan IP, Ormerod SJ (2005) The continuing challenges of testing species distribution models. *J Appl Ecol* 42:720–730. doi: 10.1111/j.1365-2664.2005.01052.x
- Vervuren PJA, Blom CWPM, De Kroon H (2003) Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. *J Ecol* 91:135–146. doi: 10.1046/j.1365-2745.2003.00749.x
- Visser EJW, Bögemann GM, Van De Steeg HM, Pierik R, Blom CWPM (2000) Flooding tolerance of *Carex* species in relation to field distribution and aerenchyma formation. *New Phytol* 148:93–103. doi: 10.1046/j.1469-8137.2000.00742.x
- Voisenek LACJ, Bailey-Serres J (2013) Flooding tolerance: O<sub>2</sub> sensing and survival strategies. *Curr Opin Plant Biol* 16:647–653. doi: 10.1016/j.pbi.2013.06.008
- Voisenek LACJ, Bailey-Serres J (2015) Flood adaptive traits and processes: an overview. *New Phytol* 206:57–73. doi: 10.1111/nph.13209
- Voisenek LACJ, Colmer TD, Pierik R, Millenaar FF, Peeters AJM (2006) How plants cope with complete submergence. *New Phytol* 170:213–226. doi: 10.1111/j.1469-8137.2006.01692.x
- Volk XK, Gattringer JP, Otte A, Harvolk-Schöning S (2018) Connectivity analysis as a tool for assessing restoration success. *Landsc Ecol* 33:371–387. doi: 10.1007/s10980-018-0611-6

- Webb JA, Wallis EM, Stewardson MJ (2012) A systematic review of published evidence linking wetland plants to water regime components. *Aquat Bot* 103:1–14. doi: 10.1016/j.aquabot.2012.06.003
- Wright AJ, De Kroon H, Visser EJW, Buchmann T, Ebeling A, Eisenhauer N, Fischer C, Hildebrandt A, Ravenek J, Roscher C, Weigelt A, Weisser W, Voisenek LACJ, Mommer L (2017) Plants are less negatively affected by flooding when growing in species-rich plant communities. *New Phytol* 213:645–656. doi: 10.1111/nph.14185
- Wright AJ, Ebeling A, De Kroon H, Roscher C, Weigelt A, Buchmann N, Buchmann T, Fischer C, Hacker N, Hildebrandt A, Leimer S, Mommer L, Oelmann Y, Scheu S, Steinauer K, Strecker T, Weisser W, Wilcke W, Eisenhauer N (2015) Flooding disturbances increase resource availability and productivity but reduce stability in diverse plant communities. *Nat Commun* 6:6092. doi: 10.1038/ncomms7092

## CHAPTER 2

### Flooding tolerance of four floodplain meadow species depends on age

Johannes P. Gattringer, Tobias W. Donath, R. Lutz Eckstein, Kristin Ludewig, Annette Otte & Sarah Harvolk-Schöning

PLoS ONE 12:e0176869 (2017). doi: 10.1371/journal.pone.0176869

#### **Abstract**

Numerous restoration campaigns focused on reestablishing species-rich floodplain meadows of Central Europe, whose species composition is essentially controlled by regular flooding. Climate change predictions expect strong alterations on the discharge regime of Europe's large rivers with little-known consequences on floodplain meadow plants. In this study, we aim to determine the effects of flooding on seedlings of different ages of four typical flood meadow species. To this end, we flooded seedlings of two familial pairs of flood meadow species of wetter and drier microhabitats for 2 weeks each, starting 2, 4, 6, and 8 weeks after seedling germination, respectively. We show that a 2-week-flooding treatment had a negative effect on performance of seedlings younger than 6 weeks. Summer floods with high floodwater temperatures may have especially detrimental effects on seedlings, which is corroborated by previous findings. As expected, the plants from wet floodplain meadow microhabitats coped better with the flooding treatment than those from drier microhabitats. In conclusion, our results suggest that restoration measures may perform more successfully if seedlings of restored species are older than the critical age of about 6 weeks before a spring flooding begins. Seasonal flow patterns may influence vegetation dynamics of floodplain meadows and should, therefore, be taken into account when timing future restoration campaigns.



## Introduction

Natural floodplains are among the ecosystems with the highest biodiversity on earth (Naiman et al. 1993; Tockner and Stanford 2002). Their azonal vegetation is shaped by a broad hydrological gradient, regular flooding and soils of diverse composition, resulting in high habitat and species diversity (Ellenberg 2009). Floodplain vegetation is also strongly influenced by humans (Allan 2004; Tockner et al. 2010). Species-rich floodplain grassland, in particular, plays a crucial role in maintaining regional biodiversity but has also experienced a dramatic decline in Central Europe (Joyce and Wade 1998) mainly due to altered hydrological conditions through river training (Brunotte et al. 2009). In particular floodplain meadows are amongst the most threatened plant communities in Europe (Joyce and Wade 1998; Riecken et al. 2006). They harbor typical and often endangered flood meadow species, also called river corridor plants, which are adapted to the specific disturbance regimes of floodplains (Burkart 2001). To maintain the diversity of these species-rich *Cnidion dubii* grasslands, protected by the EU Habitats Directive (Council Directive 92/43/EEC, habitat type 6440: alluvial meadows of river valleys of the *Cnidion dubii*) numerous restoration measures, mainly focusing on the reestablishment of rare species, have been conducted along the Rhine and Elbe Rivers, e.g., (Donath et al. 2007; Engst et al. 2016).

A challenge for such restoration projects is to consider and incorporate the effects of regular flooding, which represents a key factor in these dynamic floodplain meadows (Malanson 1993; Van Eck et al. 2004). Plant species zonation of these grasslands is mainly driven by hydrological conditions and land use (Bunn and Arthington 2002; Ludewig et al. 2014; Harvolk et al. 2015) but also on a micro-habitat scale flood sensitive species are located on elevated microsites, whereas species with higher flooding resistance occupy depressions (Vervuren et al. 2003; Jung et al. 2008). Flooding promotes recruitment of less competitive species through creation of open soil patches and suppression of flood-sensitive competitors (Hölzel and Otte 2004) and plays a crucial role for maintaining diversity of rare species through recruitment of seedlings from the soil seed bank (Hölzel and Otte 2001; Schmiede et al. 2009).

Additionally, vegetation dynamics are strongly driven by inter-annual-variation of flooding and drought (Mathar et al. 2015). Van Eck et al. (2006) showed that summer flooding predominantly determines plant zonation in flood meadows, due to the more intense impact of summer floods vs. winter floods on plants. Hence, the timing of flooding events in relation to the plant life cycle strongly influences the occurrence and distribution of plant species. In particular, seedling establishment is the critical phase in the life cycle of many plants due to high mortality through diseases, injuries,

and flooding or water deficit (Eriksson and Ehrlén 2008). The age of seedlings at which these are exposed to flooding may play a crucial role for survival (Mauchamp et al. 2001) and higher flooding tolerance may be related to species specific growth timing (Merlin et al. 2015). Nabben et al. (1999) studied the effect of flooding on juvenile vs. mature *Rumex* plants (i.e., 5 vs. 14 weeks after germination) and confirmed the higher flooding tolerance of two-months-older plants. Since the timing of flooding events during the life cycle is of crucial importance for survival, a shift in the flooding regime might have large consequences. Other experimental studies focused on the duration of flooding events but did not take the age of plants into consideration (Hosner 1958; Vervuren et al. 2003; Van Eck et al. 2004; Van Eck et al. 2006).

Flooding dynamics in present-day floodplains are highly transformed by humans and through ongoing climate change. Multiple anthropogenic stressors and their impacts on flow regime are hard to distinguish and quantify (Bunn and Arthington 2002; Tockner et al. 2010). Direct human alterations of rivers, such as construction of dams and dikes, trigger changes in water level fluctuations, which lead to alterations in terrestrial plant species composition (Leyer 2005). Furthermore, possible large-scale floodplain restoration, such as dike relocation projects or ecological flooding (also known as managed flooding) (State Ministry of the Environment Baden-Württemberg 2007; Stammel et al. 2012) could additionally alter hydrological conditions of floodplain meadows (Müller et al. 2014) and subsequently their terrestrial plant diversity.

In addition, effects of climate change are supposed to alter plant species diversity in Central Europe (Thuiller et al. 2005) through altered discharge regimes of rivers (Sperna Weiland et al. 2012). For the river Rhine, a seasonal change of the discharge regime with increasing discharge in winter and decreasing discharge in summer is projected for the current century (Middelkoop et al. 2001; Görden et al. 2010; Nilson et al. 2014). Additionally, intensity and frequency of extreme discharge events will increase (Görden et al. 2010; IPCC 2013). Accordingly, zonation of floodplain ecosystems and similarly plant composition of flood meadow habitats might change through these multiple alterations in the discharge regime (Mosner et al. 2015).

These alterations might also influence sediment deposition in the floodplain, since their soil composition strongly depends on frequency and magnitude of flooding events (Miehlich 2000). Models project considerable changes in sedimentation regime for the Rhine basin already within the current century (Asselman et al. 2003). Generally, sandy sediments can be found closest to the river channel whereas sites further away from the river are characterized by sediments with higher amounts of clay and organic matter (Miehlich 2000; Schipper et al. 2011). Changes in these patterns may

also influence vegetation since, e.g., the growth of woody floodplain plants depends on soil composition and is limited on coarse substrates after water table alterations (Mahoney and Rood 1992). However, effects of sediment grain size have not been studied with respect to flood meadow species in an experimental setup so far.

In summary, the increased unpredictability of habitat conditions under climate change induced shifts in the flow and sediment regime may act as obstacles for floodplain meadow restoration. To tackle this problem, the effects of flooding on survival and performance of plants should be investigated in more detail, to ensure success of future restoration campaigns. A recent study on flooding tolerance of wetland plants suggests that seasonal timing of flooding events plays a crucial role in flooding tolerance (Hidding et al. 2014). While the effects of flooding on adult plants have been studied before (Vervuren et al. 2003; Van Eck et al. 2004; Van Eck et al. 2006; Jung et al. 2008), studies of seedling establishment are scarce (but see Nabben et al. 1999).

Therefore, we investigate the impact of a 2-week flooding period on seedlings of different age (i.e., between 2 and 8 weeks after germination) of four characteristic species of flood meadows. To this end, we employed a completely randomized multifactorial experiment to elucidate the impact of the factors species, microhabitat, seedling age, and soil composition on the performance of seedlings. We inundated seedlings of different ages and analyzed the impact of different factors on seedling survival and establishment.

Specifically, we tested the following hypotheses: Under a 2-week flooding period,

1. older seedlings perform better than younger seedlings,
2. the performance of seedlings decreases with increased sand content, and
3. plant species from wet microhabitats perform better compared to those of dry microhabitats.

## Materials and methods

### Study species

We chose two familial pairs of floodplain meadow species with preference for wetter and drier microhabitats: *Sanguisorba officinalis* L. and *Veronica maritima* L. vs. *Sanguisorba minor* Scop. and *Veronica teucrium* L. (Table 2.1; the plant species nomenclature follows Jäger (2017)). This balanced design avoids phylogenetic bias of the results (Gitzendanner and Soltis 2000). All four species are perennials typically occurring on floodplain meadows along the Upper Rhine valley. The species charac-

**Table 2.1** Differences in the survival of four floodplain meadow species among five age groups.

species	family	micro-habitat	EIV m	chisq	df	p	survival differences				
							age2	age4	age6	age8	noFl
<i>Sanguisorba officinalis</i> L.	Rosaceae	wet	7 ~	31.5	4	<b>&lt;0.001</b>	a	a	b	c	b
<i>Sanguisorba minor</i> Scop.	Rosaceae	dry	3	94.5	4	<b>&lt;0.001</b>	a	b	c	d	c
<i>Veronica maritima</i> L.	Plantaginaceae	wet	8 ~	0.0	4	1	a	a	a	a	a
<i>Veronica teucrium</i> L.	Plantaginaceae	dry	3	66.2	4	<b>&lt;0.001</b>	ab	a	c	b	c

Differences were tested using a Wilcoxon-Mann-Whitney test (chi-square statistic), and subsequently, each paired combination was tested using a log-rank test with scores of Sun (1996) for interval censored data (Z statistic). Four groups differed in seedling age at start of flooding period (age2-age8) and one group was the unflooded control (noFl). EIV m, Ellenberg indicator value for moisture; ~, indicator for alternating moisture conditions (F value, Ellenberg et al. (1991)); chisq, chi-square value; df, degrees of freedom; p, error probability; p values < 0.05 are in bold; survival differences, significant differences (p < 0.05) in survival of plants between age groups according to log-rank test; for each species-seedling age combination: n = 20

teristic of drier microhabitats typically grow on slightly higher elevation than the species of wetter microhabitats. The plant species' preferences for wetter and drier micro niches are underlined by their Ellenberg indicator values (EIV) for moisture (F value, EIV m in Table 2.1) (Ellenberg et al. 1991). The species are target species in floodplain meadow restoration projects along the northern Upper Rhine (Donath et al. 2007). In this experiment, they serve as umbrella species in the sense of Groom et al. (2006) for the plant community of the *Cnidion dubii* meadows (Burkart et al. 2004). Here, that also comprises species from the EU Habitats Directive Annex I habitat type 6510: Lowland hay meadows. Seed material of a producer of autochthonous seeds (Rieger-Hofmann GmbH, Blaufelden-Raboldshausen, Germany) was used for the experiment.

## Experimental design

The experiment was carried out from March to July 2015. The combination of four species, two types of soil composition, and five age groups (four groups differing in seedling age at start of flooding period, and one unflooded control) with ten replicates per combination resulted in a total number of 400 experimental plants. Seeds were cold-wet stratified for 21 days at 3 °C in trays with potting soil in a climate chamber (Rumed type 3401; Rubarth Apparate GmbH, Laatzen, Germany).

Seeds germinated after 7 days (*V. teucrium* and *S. minor*) and after 10 days (*V. maritima* and *S. officinalis*) in a greenhouse (20 °C by day / 15 °C by night; photoperiod: 12 hours daily). Eleven days after germination 100 plants of every species,

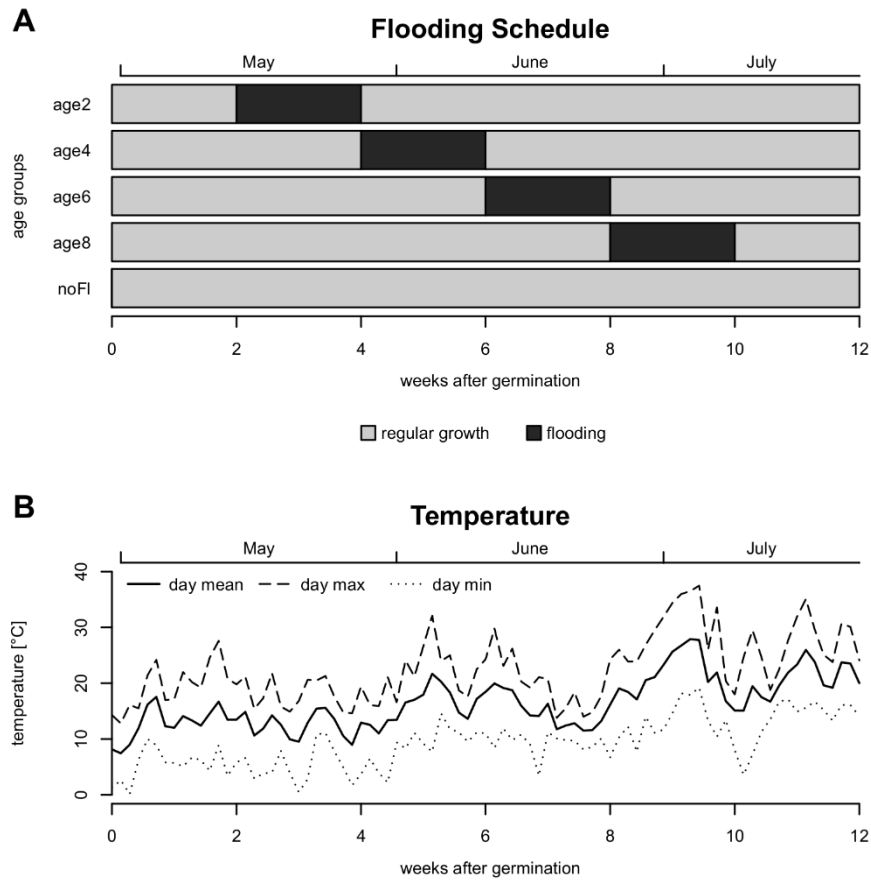
having almost the same size, were planted into pots (diameter: 9 cm on top, height: 7.8 cm). All these 400 plants had the same age of 11 days due to synchronous germination on day one.

Half of the plants were planted in a mixture of standard potting soil (F.-E. Typ P, HAWITA Gruppe GmbH, Vechta, Germany) and sand with a ratio of 3:1 and the other half in a soil:sand mixture of 1:1. We obtained nutrient equivalency in both soil treatment levels by adding slow release osmocote (Osmocote Exact Standard 3-4M, Everris International B.V., Geldermalsen, The Netherlands; 7.1% NO<sub>3</sub>-N, 8.9% NH<sub>4</sub>-N, 9% P<sub>2</sub>O<sub>5</sub>, 12% K<sub>2</sub>O) to the pots. With respect to Hidding et al. (2014) we choose an intermediate nutrient scenario for this experiment with an osmocote equivalence (i.e., nutrients in standard potting soil + osmocote) of 100 grams osmocote per square meter.

At day 15 after germination, each of the 400 pots were placed inside a 1.2 L transparent polypropylene cup (diameter: 11.4 cm on top, height: 17 cm) and randomly distributed on a paved area at the research station Linden-Leihgestern (Hesse, Germany, UTM: 32U 478260 5598300, Annex 2 Fig. 2.A1). Plants were placed under a rain shelter (height: 0.6 m, PE greenhouse grid film "Original Delta Folie SUV") to avoid accidental flooding of the cups by precipitation. Under regular growth conditions plants were watered according to their daily demand (approx. 20-50 mL day<sup>-1</sup>).

To test the response of seedlings of different age to a 2-week flooding period we performed five different treatments. Four groups of seedlings were flooded 2, 4, 6, and 8 weeks, respectively, after germination (age2, age4, age6, age8). One control group (noFl) was grown for 12 weeks without any flooding (Fig. 2.1A). The flooding procedure comprehended 2 weeks of complete inundation: the cups each with one plant pot inside were filled completely with tap water (Annex 2 Fig. 2.A1). Water levels were kept constant during the flooding period.

Survival (dead or alive) was assessed every 2 to 3 days based on physical appearance of plants: plants with green, turgid leaves and green buds were regarded as alive (Nabben et al. 1999). Total height of the plants and number of leaves were measured at the end of the experiment, i.e., after 12 weeks. We quantified specific leaf area (SLA) and aboveground biomass from measurable and living plants. For SLA, three fully expanded leaves with average size were collected of every plant, scanned and leaf area was measured with the software ImageJ (Schneider et al. 2012). The leaves were dried (48 hours at 60 °C) and weighed, SLA was calculated as leaf area per leaf dry mass (m<sup>2</sup> · kg<sup>-1</sup>). Aboveground biomass was dried (24 hours at 100 °C) and weighed and the biomass of the three leaves (SLA measurement) was added. Tem-



**Fig. 2.1** Time schedule and air temperatures for the flooding experiment of four floodplain meadow species. (A) Time schedule of age groups: four age groups with a 2-week flooding treatment starting 2, 4, 6, and 8 weeks after germination (age2, age4, age6, age8) and one unflooded control group (noFl) with regular growth through 12 weeks. (B) Temperature trend during time of the experiment (solid line: daily mean temperature, dashed line: daily minimum temperature, dotted line: daily maximum temperature). Temperature data from HLNUG (Hessian Agency for Nature Conservation, Environment and Geology, <http://www.hlnug.de>), weather station Linden (distance from experimental site: 700 m).

perature data was obtained from Hessian Agency for Nature Conservation, Environment and Geology, weather station Linden (distance from experimental site: 700 m) (HLNUG 2016).

## Analysis

In a first analysis, we tested the effects of seedling age on the cumulative seedling survival of the four species separately. To this end, a Kaplan-Meier survival analysis for interval censored data was done (i.e., measurements were taken at intervals of 2 to 3 days) (Fox 2001). We computed the non-parametric maximum likelihood esti-

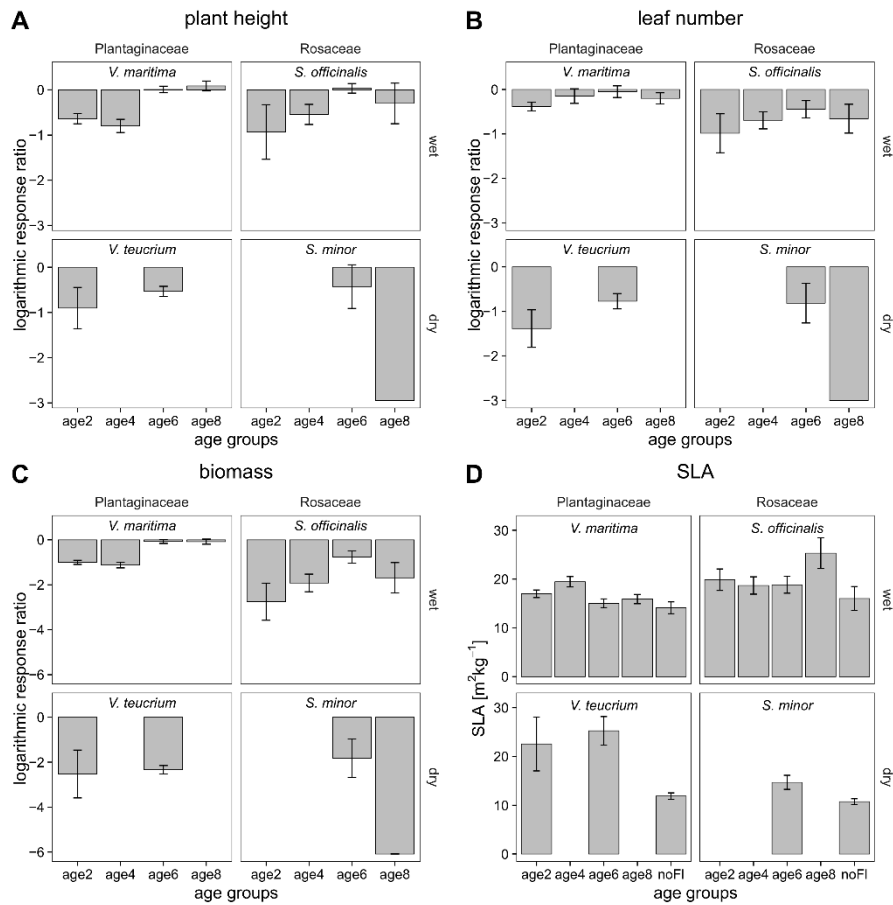
mate for the distribution from interval censored data to plot cumulative survival distributions for each species-seedling age combination with the R-package *interval* (Fay and Shaw 2010). To test for differences among species, we calculated a Wilcoxon-Mann-Whitney test with generalized Wilcoxon-Mann-Whitney scores (chi-square statistic). Subsequently, differences between treatments were tested applying a log-rank test, which uses the most commonly used log-rank scores for right-censored data and reduces to the scores of Sun (1996) for interval censored data (Z statistic).

In order to evaluate the effects of species, microhabitat, seedling age, and soil composition on survival of the plants, we computed accelerated failure time models (Kalbfleisch and Prentice 2002). We compared whether results from these analyses, containing all 400 plants, showed similar results as ANOVAs with only survived plants ( $n = 259$ ). We fitted models with six error distributions (i.e., Weibull, exponential, gaussian, logistic, log-normal and log-logistic) of which the Weibull distribution, able to deal with non-constant hazards, produced the minimum error deviance and thus was preferred (function *survreg*, R-package *survival* (Therneau 2015)). The scale parameter of this analysis describes the form of the hazard function: scale parameter  $< 1$ : risk of death decreases with time; scale parameter  $> 1$ : risk of death increases with time (Crawley 2013). To rule out other effects on survival (i.e., plant height and number of leaves before beginning of treatment) we computed Wilcoxon-Mann-Whitney tests, which did not show differences in plant height or number of leaves between surviving and dead plants.

In a next analysis, we tested for importance of the above factors on response variables: plant height, number of leaves, biomass and SLA of survived individuals using ANOVAs. We excluded dead plant individuals from this analysis to avoid detrimental effects of zero values on ANOVAs. Before analysis, the variables plant height, number of leaves and biomass were standardized using a natural logarithmic response ratio ( $RR$ ) as suggested by (Goldberg and Scheiner 2001).

$$RR = \ln(P_T/\overline{P_C})$$

This standardization of the parameter value of the treated sample ( $P_T$ ) with the mean value of the control treatment ( $\overline{P_C}$ ) for each species allows species comparisons. Effects of flooding treatments on survived plants were considered significant (i.e., different from the controls) when 95% CI did not overlap with zero in Figs 2.2A-2.2C. As SLA values already represent a ratio, we skipped the RR procedure for this response variable.



**Fig. 2.2** Performance of four floodplain meadow plant species after a 2-week flooding period. Mean ( $\pm$  95% confidence interval) logarithmic response ratio of plant height (A), leaf number (B) and biomass (C), and mean ( $\pm$  95% confidence interval) specific leaf area (SLA, D) for each species-seedling age group combination: *Veronica maritima* L., *Veronica teucrium* L., *Sanguisorba officinalis* L., and *Sanguisorba minor* Scop.; flooding started 2, 4, 6, and 8 weeks after germination (age2-age8), and control group with no flooding (noFl). Effects of flooding treatments on survived plants were considered significant (i.e., different from the controls) when 95% CI did not overlap with zero. Missing bars represent groups with a mortality of 100%.

Thereafter, one-way ANOVAs with the factor plant family were computed for every response variable, to account for potential phylogenetic effects (plant height:  $F = 0.692$ ,  $p = 0.407$ ; number of leaves:  $F = 21.14$ ,  $p < 0.001$ ; biomass:  $F = 20.55$ ,  $p < 0.001$ ; SLA:  $F = 0.012$ ,  $p = 0.914$ ). The residuals of these ANOVAs were used for the subsequent analyses. We calculated ANOVAs for each response variable (RR plant height, RR number of leaves, RR biomass and SLA) with the factors species (nested in microhabitat preference), seedling age and soil composition. To calculate the relative contribution of each factor or interaction to the total variance, we used the ratio: sum of squares of a factor/interaction divided by total sum of squares. Re-



quirements to conduct ANOVA analyses (e.g., normality) were visually checked using diagnostic plots. All statistical analyses were carried out using R (R Core Team 2016).

## Results

### Survival of plants

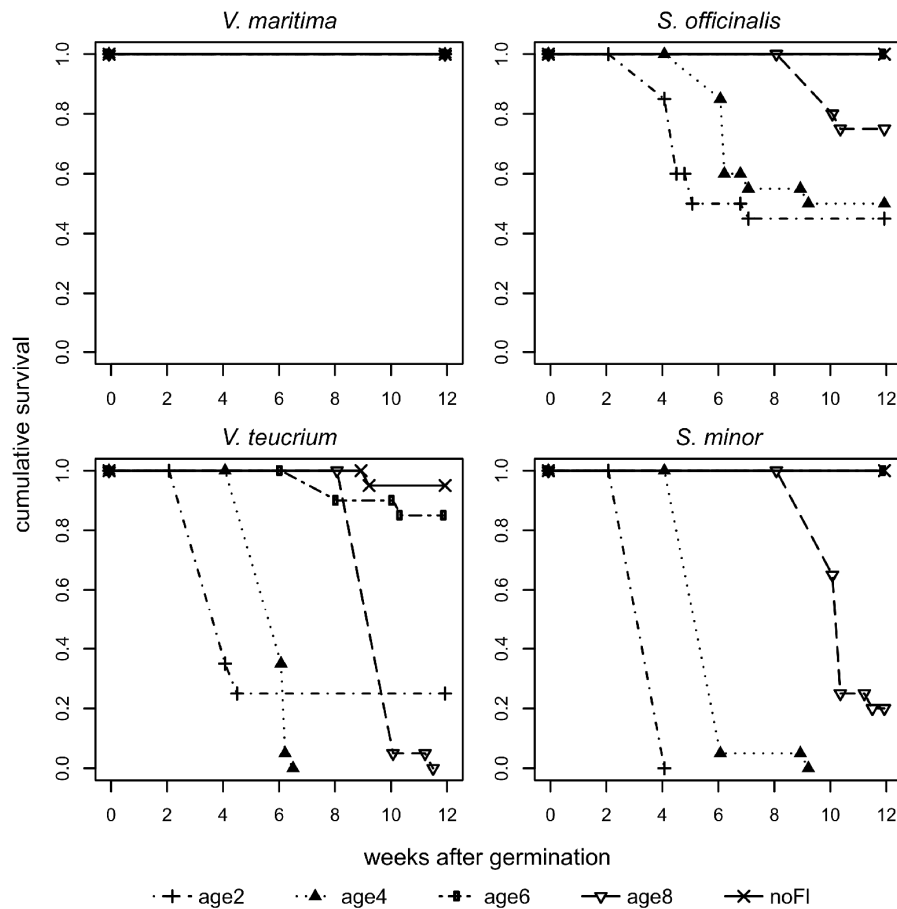
Of the 400 seedlings at the start of the experiment, 259 (64.75%) survived until the end. Survival across all treatments (4 seedling ages + control) was 14% in *V. teucrium*, 100% in *V. maritima*, 44% in *S. minor*, and 74% in *S. officinalis* (n = 100 plants per species). In the control group, i.e., no flooding treatment, overall only one individual of *V. teucrium* died (Fig. 2.3).

Results of the survival analysis showed that the 2-week flooding treatment had a significant negative effect on cumulative survival of seedlings of three plant species (i.e., *S. minor*, *S. officinalis*, and *V. teucrium*) that belonged to the age groups age2, age4, and age8 (Table 2.1). All individuals of *V. maritima* survived until the end of the experiment; hence, our flooding treatments had no effect on this species (Fig. 2.3). In the two species from dry microhabitats (*S. minor*, *V. teucrium*) two age groups showed 100% mortality (*S. minor*: age2, age4; *V. teucrium*: age4, age8). Contrarily, in species from wet microhabitats (*S. officinalis*, *V. maritima*) about half of the plants survived the flooding (e.g., *S. officinalis* lowest cumulative survival 0.45 and 0.5, Fig. 2.3).

The risk of death in our experiment decreases with age, as indicated by the scale parameter of the accelerated failure time models of 0.31 being less than one. As expected, the significance of individual factors and interactions on survival showed a similar picture as the ANOVA analyses (Table 2.2). The effects of the flooding treatment showed similar impact on plant survival and on plant performance of survived plants. The survival of the species was affected by factors microhabitat (survival rates dry: 28.75%, wet: 83.75%) and seedling age (survival rates age2: 42.5%, age4: 37.5%, age6: 96.25%, age8: 48.75%), as well as species (nested in microhabitat) and species (nested in microhabitat) x seedling age interaction (Table 2.2).

### Performance of plants

The performance of seedlings was not affected by differences in soil compositions (ANOVA analyses and accelerated failure time models: all  $p > 0.05$ ). Negative flood-



**Fig. 2.3** Effects of a 2-week flooding treatment on survival of four floodplain meadow plant species. Cumulative survival of *Veronica maritima* L., *Veronica teucrium* L., *Sanguisorba officinalis* L., and *Sanguisorba minor* Scop. after a 2-week flooding treatment, starting 2, 4, 6, and 8 weeks, respectively, after germination (age2-age8), and a control group with no flooding (noFl). age2, dot-dashed line & plus; age4, dotted line & filled triangle point up; age6, two-dashed line & circle; age8, long-dashed line & triangle point down; noFl, solid line & cross.

ing effects on plant growth i.e., reduced plant height, leaf number, and biomass production were significant for age groups age2 and age4 of all plants except *S. minor*, where both groups showed 100% mortality (Figs 2.2A-2.2C). This effect did not clearly decrease with age, but for the two species from wet microhabitats (i.e., *V. maritima* and *S. officinalis*) fitness of flooded plants was mostly not significantly different from the control for older seedlings (6 and 8 weeks after germination). Similarly, a slight but non-significant trend of increasing plant height with age was visible for *V. maritima* and *S. officinalis* (Fig. 2.2A).

**Table 2.2** Performance of four floodplain meadow plant species after a 2-week flooding period

	survival			plant height				number of leaves			
	df	dev	p	df	F	p	vc	df	F	p	vc
microhabitat (M)	1	96.1	<0.001	1	18.1	<0.001	5.6	1	53.2	<0.001	17.2
seedling age (A)	4	270.3	<0.001	3	23.1	<0.001	21.4	3	12	<0.001	11.7
soil (S)	1	1.5	0.214	1	0.6	0.427	0.2	1	0.9	0.347	0.3
species(microhabitat) [Sp(M)]	6	55.7	<0.001	2	1.2	0.302	0.7	2	0.6	0.532	0.4
M x A	4	1.5	0.823	2	29.3	<0.001	18.1	2	22.5	<0.001	14.5
M x S	1	1.4	0.234	1	0.4	0.512	0.1	1	1.9	0.165	0.6
A x S	4	8.2	0.084	3	1.2	0.326	1.1	3	1.6	0.188	1.6
Sp(M) x A	24	56.4	<0.001	3	2.4	0.072	2.2	3	0.3	0.798	0.3
Sp(M) x S	6	0.3	0.999	2	0.8	0.462	0.5	2	0.6	0.555	0.4
M x A x S	4	1.2	0.884	2	0.7	0.500	0.4	2	2.8	0.065	1.8
Sp(M) x A x S	24	1.0	1.000	3	1.4	0.239	1.3	3	0.9	0.443	0.9
Residuals	319			156			48.2	156			50.4

	biomass				SLA			
	df	F	p	vc	df	F	p	vc
microhabitat (M)	1	82.4	<0.001	20.9	1	13.5	<0.001	2.4
seedling age (A)	3	22.2	<0.001	16.9	4	30.7	<0.001	22.1
soil (S)	1	0	0.976	0	1	2.2	0.135	0.4
species(microhabitat) [Sp(M)]	2	4	<b>0.020</b>	2	2	45.4	<0.001	16.4
M x A	2	30.2	<0.001	15.3	2	16.9	<0.001	6.1
M x S	1	1.4	0.232	0.4	1	0.1	0.718	0
A x S	3	0.4	0.747	0.3	4	0.5	0.706	0.4
Sp(M) x A	3	3	<b>0.030</b>	2.3	5	13	<0.001	11.7
Sp(M) x S	2	0.5	0.607	0.3	2	0.1	0.904	0
M x A x S	2	2.2	0.117	1.1	2	0.4	0.647	0.2
Sp(M) x A x S	3	1.2	0.314	0.9	5	0.6	0.696	0.5
Residuals	156			39.6	220			39.7

Effects of factors microhabitat, species nested in microhabitat, seedling age, and soil composition on the survival of all plant individuals, and on plant height (logarithmic response ratio), number of leaves (logarithmic response ratio), biomass (logarithmic response ratio), and specific leaf area (SLA) of survived plant individuals were tested performing a likelihood-ratio test of an accelerated failure time model using a Weibull error distribution and four ANOVA Analyses. df, degrees of freedom; dev, deviance; F, variance ratio; p, error probability; vc (%), relative contribution of individual factors and their interactions to total variance; p values < 0.05 are written in bold.

Microhabitat preference of the species, as reflected in Ellenberg indicator values (EIV) for moisture, had a significant impact on plants (over all four response variables, and on survival, Table 2.2): Plants from wet microhabitats showed less reduction in plant height and leaf number, higher biomass, and slightly higher SLA than plants from drier microhabitats (all  $p < 0.001$ ).

At the end of the experiment, the seedlings flooded at younger age (i.e., age groups age2 and age4) were smaller, had fewer leaves, and lower biomass than older seedlings (except for *S. minor*). Thus, also the factor seedling age explained a high amount of the total variance (vc, Table 2.2). Similarly, in the accelerated failure time models analysis, we found a significant effect of seedling age on the survival of the plants (Table 2.2).

Response of plants on flooding treatments was species-dependent, as indicated by the significance of species (nested in microhabitat) x seedling age interaction in accelerated failure time models and ANOVAs (Table 2.2). Inundated plants produced thinner leaves, which resulted in slightly higher SLA (not significant) compared to non-flooded plants from the control group (Fig. 2.2D).

## Discussion

### The effects of age on the survival and performance of seedlings in response to flooding

Our experiment revealed that 2 weeks of flooding lowered survival of three of the four tested species (i.e., *S. officinalis*, *S. minor* and *V. teucrium*) and that survival increased with the age of the seedlings, as risk of death decreased. Our first hypothesis that under a 2-week flooding period, older seedlings perform better than younger seedlings, therefore was accepted. These results are in line with a study by Nabben et al. (1999), who found that juvenile plants of three *Rumex* species showed lower survival (approx. by factor four) than mature plants. In accordance to this study, we expected survival increasing with age of the seedlings over individual age groups. However, for the oldest group, with flooding start at an age of 8 weeks after germination, survival was lower than expected. This outcome can be explained by particularly high temperatures during this flooding treatment (age8, Fig. 2.1B). Summer floods may result in heating of the slow flowing, ponded water on the floodplain meadows and this probably also happened to our experimental plants. This rise in water temperature most likely forced additional damage of flooded plants, as warm tempera-

tures increase enzyme activity and limit oxygen solubility (Rapacz et al. 2014). Detrimental flooding effects on mature grasses are known to be greater at high water temperature (30 °C) compared to low temperature (10 °C) floods (Beard and Martin 1970). Hence, summer floods are likely more harmful than flooding events earlier in the year. Likewise, Van Eck et al. (2006) showed that mainly summer flooding defines zonation of plants on flood meadows. Our data may suggest an age threshold for flood meadow species from wet microhabitats between 4 and 6 weeks after which the negative effects of a 2-week flooding event appears to be significantly reduced. Likewise, Hidding et al. (2014) recently suggested that flooding outcome (i.e., promotion of plant growth vs. severe damaging of plants) depends strongly on the timing of flooding. In their experiment, wetland plants, with an age of approx. 5 weeks at the start of the flooding treatment, showed elongation of plant growth (7 out of 8 species) but also unclear responses in horizontal expansion and biomass production after flooding. Also for *Phragmites australis* seedlings the tolerance to submergence increased with age (Mauchamp et al. 2001), hence this effect may be ubiquitous for plants from riparian ecosystems.

### **The effects of substrate on the survival and performance of seedlings in response to flooding**

Differences in soil composition (i.e., soil:sand ratio of 3:1 vs. 1:1) had no effect on the response variables (Table 2.2). Thus, our second hypothesis that under a 2-week flooding period, the performance of the seedlings decreases with increased sand content, was rejected. Interestingly, Lenson et al. (1999) showed that wetland species produce more biomass on soils with organic sediments compared to mineral sediments. They concluded that this was caused by the low nutrient availability in the mineral-sediment soil. In our study, maintaining nutrient equivalence in the two soil:sand ratio groups resulted in similar plant performance, which supports the conclusions of Lenson et al. (1999). Likewise, in a study on floodplains along the Middle Elbe, sand content only weakly explains species composition (Leyer 2006).

### **Differences in the survival and performance of seedlings from wet vs. dry microhabitats in response to flooding**

We found evidence that under flooding treatment, species preferring wet microhabitats grow higher and survive longer compared to species from dry microhabitats. This confirmed our third hypothesis that under a 2-week flooding period, plant species from wet microhabitats perform better compared to those of dry microhabitats. Higher survival and plant growth of *V. maritima* compared to *S. officinalis* within the wet

microhabitat is consistent with differences in Ellenberg indicator values between the two species (Table 2.1) (Ellenberg et al. 1991). More generally, our findings cohere with the expectations that flood sensitive species are located on higher parts of the floodplain where flooding impacts are limited. In contrast, flood tolerant species survive at areas with more frequent flooding at lower elevations (Van Eck et al. 2004; Lenssen and De Kroon 2005; Van Eck et al. 2006). Likewise, leaf thickness of plants varies between species with different microhabitat preferences. SLA of plants adapted to wet microhabitats is higher than of plants from dry microhabitats (Table 2.2). Also Koike et al. (2003) found contrasting SLA values for birch species with different microhabitat preferences under wet soil moisture conditions. In addition, our result that leaf plasticity differs between treatment and control (i.e., SLA of flooded plants is slightly higher than for plants from control group, Fig. 2.2D) is in accordance with previous findings. Plants under submergence develop thinner, elongated leaves and therefore show increased SLA (for review see (Mommer and Visser 2005)).

### **Synopsis for restoration management**

From a restoration ecological perspective, our finding that seedlings of flood-meadow species respond differently to flooding events at young age show the difficulties of measures that aim to reestablish floodplain vegetation (e.g., via the transfer of seed-containing plant material) (Kiehl et al. 2010). The forecasted increase in extreme discharge events owing to climate change will simultaneously raise the risk for restoration measures in terms of costs and logistic effort. To increase restoration success, habitat requirements of the individual target plant species and microhabitat characteristics of restoration sites have to match. Habitat-suitability maps on a microhabitat scale for the target species could incorporate all these factors and enhance restoration planning (Guisan et al. 2013). In case of planning large-scale restoration projects, especially regarding ecological (i.e., prescribed) flooding, our findings should also be taken into account. After a floodplain restorations, the schedule of gate openings at ecological flooding sites should be adapted to germination timing of target species to enhance survival and establishment of target species.

### **Conclusions**

In conclusion, our results demonstrated the importance of seedling age and microhabitat preference of plants on their flooding tolerance, whereas soil composition had no effect. Based on our data, we predict that for future restoration measures of floodplain meadows (e.g., the transfer of freshly cut seed-containing plant material) the restoration success after a medium flooding event will be higher, if the plants have

reached the critical threshold age of about 6 weeks after germination. Besides, flooding in summer may also lead to stronger damages of plants due to higher floodwater temperatures. Vegetation of floodplain meadows indeed is affected by seasonal flow patterns (for review see (Greet et al. 2011)). All these aspects demonstrate the increasing vulnerabilities of floodplain meadow species under the predicted alterations of climatic and thus hydrological conditions (Mosner et al. 2015). Hence, the complexity regarding timing of floodplain meadow restorations and of conservation planning in floodplain landscapes in general is increasing.

## Acknowledgments

We thank Josef Scholz-vom Hofe and Laura Düpre for assistance in growing the plants and data collection. We are grateful to two anonymous reviewers, whose comments improved the manuscript.

## Funding

This research was funded by the Deutsche Bundesstiftung Umwelt DBU (Project No. 31612-33/0; [www.dbu.de](http://www.dbu.de)). The funder had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

## Competing Interest

The authors have declared that no competing interests exist.

## References

- Allan JD (2004) Landscapes and Riverscapes: The Influence of Land Use on Stream Ecosystems. *Annu Rev Ecol Evol Syst* 35:257–284. doi: 10.1146/annurev.ecolsys.35.120202.110122
- Asselman NEM, Middelkoop H, van Dijk PM (2003) The impact of changes in climate and land use on soil erosion, transport and deposition of suspended sediment in the River Rhine. *Hydrol Process* 17:3225–3244. doi: 10.1002/hyp.1384
- Beard J, Martin DP (1970) Influence of Water Temperature on Submersion Tolerance of Four Grasses. *Agron J* 62:257–259. doi: 10.2134/agronj1970.00021962006200020024x

- Brunotte E, Dister E, Günther-Diringer D, Koenzen U, Mehl D (2009) Flussauen in Deutschland. Erfassung und Bewertung des Auenzustandes (Floodplains in Germany. Recording and evaluation of floodplain conditions). *Naturschutz Biol Vielfalt* 87:1–141
- Bunn SE, Arthington AH (2002) Basic Principles and Ecological Consequences of Altered Flow Regimes for Aquatic Biodiversity. *Environ Manage* 30:492–507. doi: 10.1007/s00267-002-2737-0
- Burkart M (2001) River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. *Glob Ecol Biogeogr* 10:449–468. doi: 10.1046/j.1466-822x.2001.00270.x
- Burkart M, Dierschke H, Hölzel N, Nowak B, Fartmann T (2004) Molinio-Arrhenatheretea (E1) - Kulturgrasland und verwandte Vegetationstypen (Molinio-Arrhenatheretea E1 - Cultural grassland and related vegetation types). *Synop Pflanzengesellschaften Dtschl* 1–103.
- Crawley MJ (2013) *The R Book*, 2nd edn. John Wiley & Sons, Ltd, Chichester, UK
- Donath TW, Bissels S, Hölzel N, Otte A (2007) Large scale application of diaspore transfer with plant material in restoration practice – Impact of seed and microsite limitation. *Biol Conserv* 138:224–234. doi: 10.1016/j.biocon.2007.04.020
- Ellenberg H (2009) *Vegetation Ecology of Central Europe*, 4th edn. Cambridge University Press, Cambridge, New York
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1991) *Zeigerwerte von Pflanzen in Mitteleuropa (Indicator values of plants in Central Europe)*, 3rd edn. Goltze, Göttingen
- Engst K, Baasch A, Erfmeier A, Jandt U, May K, Schmiede R, Bruelheide H (2016) Functional community ecology meets restoration ecology: Assessing the restoration success of alluvial floodplain meadows with functional traits. *J Appl Ecol* 53:751–764. doi: 10.1111/1365-2664.12623
- Eriksson O, Ehrlén J (2008) Seedling recruitment and population ecology. In: Leck MA, Parker VT, Simpson R (eds) *Seedling Ecology and Evolution*. Cambridge University Press, Cambridge,
- Fay MP, Shaw PA (2010) Exact and Asymptotic Weighted Logrank Tests for Interval Censored Data: The interval R package. *J Stat Softw* 36:1–34.
- Fox GA (2001) Failure-time analysis: emergence, flowering, survivorship, and other waiting times. In: Scheiner SM, Gurevitch J (eds) *Design and Analysis of Ecological Experiments*, 2nd edn. Oxford University Press, Oxford, New York, pp 235–266
- Gitzendanner MA, Soltis PS (2000) Patterns of genetic variation in rare and widespread plant congeners. *Am J Bot* 87:783–792. doi: 10.2307/2656886
- Goldberg DE, Scheiner SM (2001) ANOVA and ANCOVA: field competition experiments. In: Scheiner SM, Gurevitch J (eds) *Design and Analysis of Ecological Experiments*, 2nd edn. Oxford University Press, Oxford, New York, pp 77–98



- Görge K, Beersma J, Brahmner G, Buiteveld H, Carambia M, de Keizer O, Krahe P, Nilson E, Lammersen R, Perrin C, Volken D (2010) Assessment of climate change impacts on discharge in the Rhine River Basin: results of the RheinBlick2050 project. CHR, Lelystad
- Greet J, Angus Webb J, Cousens RD (2011) The importance of seasonal flow timing for riparian vegetation dynamics: a systematic review using causal criteria analysis: Effects of seasonal flow timing on riparian flora. *Freshw Biol* 56:1231–1247. doi: 10.1111/j.1365-2427.2011.02564.x
- Groom MJ, Meffe GK, Carroll CR (2006) *Principles of Conservation Biology*, 3rd edn. Sinauer Associates, Inc., Sunderland
- Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. *Ecol Lett* 16:1424–1435. doi: 10.1111/ele.12189
- Harvolk S, Symmank L, Sundermeier A, Otte A, Donath TW (2015) Human impact on plant biodiversity in functional floodplains of heavily modified rivers – A comparative study along German Federal Waterways. *Ecol Eng* 84:463–475. doi: 10.1016/j.ecoleng.2015.09.019
- Hidding B, Sarneel JM, Bakker ES (2014) Flooding tolerance and horizontal expansion of wetland plants: Facilitation by floating mats? *Aquat Bot* 113:83–89. doi: 10.1016/j.aquabot.2013.11.003
- HLNUG (2016) Luftmessstation Linden (Weather station Linden). Hessian Agency for Nature Conservation, Environment and Geology. <http://www.hlnug.de/?id=9231&station=1005>
- Hölzel N, Otte A (2004) Inter-annual variation in the soil seed bank of flood-meadows over two years with different flooding patterns. *Plant Ecol* 174:279–291. doi: 10.1023/B:VEGE.0000049108.04955.e2
- Hölzel N, Otte A (2001) The impact of flooding regime on the soil seed bank of flood-meadows. *J Veg Sci* 12:209–218. doi: 10.2307/3236605
- Hosner JF (1958) The Effects of Complete Inundation upon Seedlings of Six Bottomland Tree Species. *Ecology* 39:371–373. doi: 10.2307/1931886
- IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA
- Jäger EJ (ed) (2017) *Rothmaler - Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband [Fieldflora of Germany, vascular plants, basic volume]*, 21st edn. Springer Spektrum, Berlin
- Joyce CB, Wade PM (1998) Wet Grasslands: A European Perspective. In: Joyce CB, Wade PM (eds) *European Wet Grasslands: Biodiversity, Management and Restoration*. Wiley, Chichester, UK, pp 1–12

- Jung V, Hoffmann L, Muller S (2008) Ecophysiological responses of nine floodplain meadow species to changing hydrological conditions. *Plant Ecol* 201:589–598. doi: 10.1007/s11258-008-9508-9
- Kalbfleisch JD, Prentice RL (2002) Rank Regression and the Accelerated Failure Time Model. In: Kalbfleisch JD, Prentice RL (eds) *The Statistical Analysis of Failure Time Data*, 2nd edn. John Wiley & Sons, Inc., Hoboken, New Jersey, pp 31–51
- Kiehl K, Kirmer A, Donath TW, Rasran L, Hölzel N (2010) Species introduction in restoration projects – Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic Appl Ecol* 11:285–299. doi: 10.1016/j.baae.2009.12.004
- Koike T, Kitao M, Quoreshi AM, Matsuura Y (2003) Growth characteristics of root-shoot relations of three birch seedlings raised under different water regimes. *Plant Soil* 255:303–310. doi: 10.1023/A:1026199402085
- Lenssen JPM, De Kroon H (2005) Abiotic constraints at the upper boundaries of two *Rumex* species on a freshwater flooding gradient. *J Ecol* 93:138–147. doi: 10.1111/j.1365-2745.2004.00957.x
- Lenssen JPM, Menting FBJ, van der Putten WH, Blom CWPM (1999) Effects of sediment type and water level on biomass production of wetland plant species. *Aquat Bot* 64:151–165. doi: 10.1016/S0304-3770(99)00012-1
- Leyer I (2005) Predicting plant species' responses to river regulation: the role of water level fluctuations. *J Appl Ecol* 42:239–250. doi: 10.1111/j.1365-2664.2005.01009.x
- Leyer I (2006) Dispersal, diversity and distribution patterns in pioneer vegetation: The role of river-floodplain connectivity. *J Veg Sci* 17:407–416. doi: 10.1111/j.1654-1103.2006.tb02461.x
- Ludewig K, Korell L, Löffler F, Scholz M, Mosner E, Jensen K (2014) Vegetation patterns of floodplain meadows along the climatic gradient at the Middle Elbe River. *Flora - Morphol Distrib Funct Ecol Plants* 209:446–455. doi: 10.1016/j.flora.2014.04.006
- Mahoney JM, Rood SB (1992) Response of a hybrid poplar to water table decline in different substrates. *For Ecol Manag* 54:141–156. doi: 10.1016/0378-1127(92)90009-X
- Malanson GP (1993) *Riparian Landscapes*. Cambridge University Press, Cambridge
- Mathar W, Kleinebecker T, Hölzel N (2015) Environmental variation as a key process of co-existence in flood-meadows. *J Veg Sci* 26:480–491. doi: 10.1111/jvs.12254
- Mauchamp A, Blanch S, Grillas P (2001) Effects of submergence on the growth of *Phragmites australis* seedlings. *Aquat Bot* 69:147–164. doi: 10.1016/S0304-3770(01)00135-8
- Merlin A, Bonis A, Damgaard CF, Mesléard F (2015) Competition is a strong driving factor in wetlands, peaking during drying out periods. *PLoS ONE* 10:e0130152. doi: 10.1371/journal.pone.0130152
- Middelkoop H, Daamen K, Gellens D, Grabs W, Kwadijk JC, Lang H, Parmet BW, Schädler B, Schulla J, Wilke K (2001) Impact of climate change on hydrological regimes and water re-

- sources management in the Rhine basin. *Clim Change* 49:105–128. doi: 10.1023/A:1010784727448
- Miehlich G (2000) Eigenschaften, Genese und Funktionen von Böden in Auen Mitteleuropas (Properties, genesis and functions of soils in floodplains in Central Europe). In: Friese K, Witter B, Miehlich G, Rode M (eds) *Stoffhaushalt von Auenökosystemen: Böden und Hydrologie, Schadstoffe, Bewertungen (Biogeochemical cycles of floodplain ecosystems: soils and hydrology, pollutants, assessment)*, 1st edn. Springer, Berlin, Heidelberg, pp 3–17
- Mommer L, Visser EJW (2005) Underwater photosynthesis in flooded terrestrial plants: a matter of leaf plasticity. *Ann Bot* 96:581–589. doi: 10.1093/aob/mci212
- Mosner E, Weber A, Carambia M, Nilson E, Schmitz U, Zelle B, Donath T, Horchler P (2015) Climate change and floodplain vegetation—future prospects for riparian habitat availability along the Rhine River. *Ecol Eng* 82:493–511. doi: 10.1016/j.ecoleng.2015.05.013
- Müller M, Pander J, Stammel B, Gelhaus M, Cyffka B (2014) Synthese und Schlussfolgerungen zu den Ergebnissen des Monitorings in MONDAU (Synthesis and conclusions on the results of monitoring in MONDAU). *Auenmagazin* 7:38–42.
- Nabben RHM, Blom CWPM, Voeselek LACJ (1999) Resistance to complete submergence in *Rumex* species with different life histories: the influence of plant size and light. *New Phytol* 144:313–321. doi: 10.1046/j.1469-8137.1999.00519.x
- Naiman RJ, Decamps H, Pollock M (1993) The Role of Riparian Corridors in Maintaining Regional Biodiversity. *Ecol Appl* 3:209–212. doi: 10.2307/1941822
- Nilson E, Krahe P, Lingemann I, Horsten T, Klein B, Carambia M, Larina M (2014) Auswirkungen des Klimawandels auf das Abflussgeschehen und die Binnenschifffahrt in Deutschland (Climate change impacts on the runoff and inland water transportation in Germany), Schlussbericht KLIWAS-Projekt 4.01 (Final Report KLIWAS-Project 4.01). KLIWAS-43/2014. BfG (German Federal Institute of Hydrology), Koblenz
- R Core Team (2016) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>
- Rapacz M, Ergon Å, Höglind M, Jørgensen M, Jurczyk B, Østrem L, Rognli OA, Tronsmo AM (2014) Overwintering of herbaceous plants in a changing climate. Still more questions than answers. *Plant Sci* 225:34–44. doi: 10.1016/j.plantsci.2014.05.009
- Riecken U, Finck P, Raths U, Schröder E, Ssymank A (2006) Rote Liste der gefährdeten Biotop-typen Deutschlands. Zweite fortgeschriebene Fassung (Red list of threatened habitat types in Germany. Second updated version). *Naturschutz Biol Vielfalt* 34:1–318.
- Schipper AM, Lotterman K, Leuven RSEW, Ragas AMJ, de Kroon H, Hendriks AJ (2011) Plant communities in relation to flooding and soil contamination in a lowland Rhine River floodplain. *Environ Pollut* 159:182–189. doi: 10.1016/j.envpol.2010.09.006
- Schmiede R, Donath TW, Otte A (2009) Seed bank development after the restoration of alluvial grassland via transfer of seed-containing plant material. *Biol Conserv* 142:404–413. doi: 10.1016/j.biocon.2008.11.001

- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nat Methods* 9:671–675. doi: 10.1038/nmeth.2089
- Sperna Weiland FC, Van Beek LPH, Kwadijk JCJ, Bierkens MFP (2012) Global patterns of change in discharge regimes for 2100. *Hydrol Earth Syst Sci* 16:1047–1062. doi: 10.5194/hess-16-1047-2012
- Stammel B, Cyffka B, Geist J, Müller M, Pander J, Blasch G, Fischer P, Gruppe A, Haas F, Kilg M, Lang P, Schopf R, Schwab A, Utschik H, Weißbrod M (2012) Floodplain restoration on the Upper Danube (Germany) by re-establishing water and sediment dynamics: a scientific monitoring as part of the implementation. *River Syst* 20:55–70. doi: 10.1127/1868-5749/2011/020-0033
- State Ministry of the Environment Baden-Württemberg (2007) *The Integrated Rhine Programme: Flood control and restoration of former floodplains along the Upper Rhine*, 2nd edn. Stuttgart
- Sun J (1996) A non-parametric test for interval-censored failure time data with application to AIDS studies. *Stat Med* 15:1387–1395. doi: 10.1002/(SICI)1097-0258(19960715)15:13<1387::AID-SIM268>3.0.CO;2-R
- Therneau TM (2015) *A Package for Survival Analysis in S*. version 2.38.
- Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci U S A* 102:8245–8250. doi: 10.1073/pnas.0409902102
- Tockner K, Pusch M, Borchardt D, Lorang MS (2010) Multiple stressors in coupled river–floodplain ecosystems. *Freshw Biol* 55:135–151. doi: 10.1111/j.1365-2427.2009.02371.x
- Tockner K, Stanford JA (2002) Riverine flood plains: present state and future trends. *Environ Conserv* 29:308–330. doi: 10.1017/S037689290200022X
- Van Eck WHJM, Lenssen JPM, Van De Steeg HM, Blom CWPM, 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. doi: 10.1007/s10750-005-1905-7
- Van Eck WHJM, Van De Steeg HM, Blom CWPM, 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. doi: 10.1111/j.0030-1299.2004.13083.x
- Vervuren PJA, Blom CWPM, De Kroon H (2003) Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. *J Ecol* 91:135–146. doi: 10.1046/j.1365-2745.2003.00749.x

## Annex 2

**Dataset** Dataset of the experiment. Available online:  
[doi.org/10.1371/journal.pone.0176869.s002](https://doi.org/10.1371/journal.pone.0176869.s002)



**Fig. 2.A1** Photograph of experimental setup. Photograph showing experimental plant pots placed inside of 1.2L transparent polypropylene cups and distributed randomly on a paved area at the research station Linden-Leihgestern (Hesse, Germany, UTM: 32U 478260 5598300) in May 2015. Photo: Johannes P. Gattringer

## CHAPTER 3

### Interaction between depth and duration matters: flooding tolerance of 12 floodplain meadow species

Johannes P. Gattringer, Kristin Ludewig, Sarah Harvolk-Schöning, Tobias W. Donath & Annette Otte

*Plant Ecology* 219:973–984 (2018). doi: 10.1007/s11258-018-0850-2

#### **Abstract**

In riparian landscapes, regular flooding plays a crucial role in the distribution and diversity of plant species. Particularly in floodplain grassland, the microrelief, which is often the result of riverine sedimentation through flooding, leads to differing flooding depths and durations on a microscale, with little-known impacts on plants. Here, we aim to reveal the effects of flooding duration and flooding depth, as well as their interaction, on seedlings of 12 floodplain meadow plant species. To this end, we performed flooding procedures for 2 and 4 weeks with no, partial and complete submergence using seedlings of floodplain meadow species in six familial pairs with a preference for relatively wetter or drier microhabitats. We show that an increased flooding duration and flooding depth negatively affect the performance of seedlings. The interactive effect of these two factors appears to play an essential role in the flooding tolerance of plant species. In conclusion, our results suggest that the studied factors and their interaction have high importance in determining the flooding tolerance of floodplain meadow plant species. Despite its crucial function, the effect of the depth  $\times$  duration interaction seems to be underestimated in experimental studies focusing on flooding effects in plants. Thus, this interaction, as well as its combination with other factors, should be studied in more detail to further understand plant responses to flooding events.

## Introduction

Regular flooding substantially affects the distribution and diversity of species in riparian and wetland ecosystems in multiple ways (Malanson 1993; Silvertown et al. 1999); it facilitates the establishment of less competitive species by means of the exposure of bare soil for germination and inhibits flood-intolerant competitors (Hölzel and Otte 2004). From an ecophysiological perspective, flooding represents an environmental stress with detrimental effects on the survival and growth of plants in many ecosystems (Bailey-Serres and Voesenek 2008). However, as many plant species depend on specific conditions with more or less regular flooding, the loss of such habitats resulted in a strong decline in these species (Joyce and Wade 1998). In Europe and North America, large amounts of riparian habitat have been degraded by human actions, such as river regulation (Tockner and Stanford 2002). Indeed, species-rich floodplain meadows, such as those of the type *Cnidion dubii*, are among the most threatened habitat types in Central Europe (Joyce and Wade 1998; Finck et al. 2017) and are therefore protected by the EU Habitats Directive. These grasslands harbor numerous, often endangered, plant species that are able to cope with the particular disturbance regimes (e.g., flooding) of floodplains (Burkart 2001). For the protection of these species, specific knowledge regarding their flooding tolerances, and moreover their niches, is essential (Engst et al. 2016). On a micro-habitat scale, these grassland species segregate in accordance to their hydrological niches (Silvertown et al. 1999; Silvertown et al. 2015); species with higher flooding tolerance are located in depressions, whereas more flood-sensitive species occur at higher elevations (Vervuren et al. 2003; Jung et al. 2008). Habitat-specific germination strategies were found in 20 floodplain grassland species indicative of wet or dry habitats (Ludewig et al. 2014). Nevertheless, despite their fine ecological differentiation (along a microhabitat preference gradient), those species occur in basically identical habitats due to the microrelief in the meadows (Mathar et al. 2015).

Flooding is a phenomenon with multiple components that all influence plants (Vervuren et al. 2003). The components duration, depth and timing of flooding events (in addition to several others, e.g., floodwater temperature, suspended load, and flooding frequency) are the key factors affecting plant growth in wetland ecosystems (Cronk and Fennessy 2001; Vervuren et al. 2003; Magee and Kentula 2005). Several studies have investigated the separate impacts of the components flooding duration and flooding depth; in general, in grassland species, plant survival and biomass decrease with increasing flooding duration (Blom et al. 1994; Van Eck et al. 2004) and increasing water depth during a flooding event (Vervuren et al. 2003). The

combined effect of these two factors among floodplain meadow species has not yet been studied in an experiment under controlled conditions. Van Eck et al. (2005) showed that interactions between flooding duration and oxygen concentration and between flooding duration and water temperature have significant influences on biomass reduction in three plant species under flooding (*Rumex crispus*, *Rumex acetosa*, and *Daucus carota*). Hence, the interactive effect of two or more components during flooding is of particular importance to plant growth. Likewise, Madsen and Sand-Jensen (1994) demonstrated that multifactor limitations of growth under submergence are a common phenomenon in flooded (aquatic) plants. To our knowledge, the effect of duration has been disregarded in flooding depth experiments until now, which might have led to the differing findings in the literature; in a systematic review of wetland plant studies focusing on water regime, Webb et al. (2012) concluded that shoot length increases with increasing water depth, whereas belowground biomass decreases. At the same time, they concluded that the total plant biomass neither increased nor decreased with increasing water depth, and the evidence for aboveground biomass was inconsistent (Webb et al. 2012). Nevertheless, a study focusing on four riparian grassland species from the Rhine River demonstrated a significant decline in survival with increasing flooding depth (Vervuren et al. 2003). Similarly, *Phragmites australis* showed decreasing biomass production and length growth with a deeper experimental flooding depth (Mauchamp et al. 2001). The interaction between flooding depth and duration seems to play a crucial role, which previous studies have largely neglected (e.g., Byun et al. 2017; Nicol et al. 2018).

Here, we provide such an analysis for 12 species from species-rich floodplain meadows with differing sensitivities to flooding and high nature conservation value. We aim toward a better understanding of the interplay between flooding duration and flooding depth in combination with the microhabitat preference of the species. We study the response of young flooded meadow plants to partial and complete submergence for a duration of 2 and 4 weeks. Therefore, we performed a multi-factorial flooding experiment to analyze the main effects and interactions of the factors flooding duration, flooding depth, and microhabitat preference on several performance parameters of plants. Since we expected constraints to plant performance in association with increasing flooding depth and duration, as well as an influence of their interaction, we tested the following hypotheses:

1. The combination of the expected (negative) effects of increased flooding depth and flooding duration results in non-additive (i.e., interactive) detrimental effects on plants.



2. Flooded plants with a preference for wet microhabitats show better performance than those with a preference for dry microhabitats.

## Materials and methods

### Study species

The focal plant species here (Table 3.1) have been target species in floodplain restoration projects along the Upper Rhine since the 1980s (Donath et al. 2007). In this study, they act as umbrella species (according to Groom et al. 2006) for the plant community of *Cnidion dubii* grassland (Burkart et al. 2004), which is also under protection by the EU Habitats Directive (Council Directive 92/43/EEC Annex I; habitat type 6440: alluvial meadows of river valleys of the *Cnidion dubii*). Furthermore, the experimental species are representative of the habitat type 6510: lowland hay meadows. We selected six congeneric pairs of floodplain meadow species characteristic of wet vs. dry microhabitats (Table 3.1). The phylogenetically balanced design improves the explanatory power of the results (Gitzendanner and Soltis 2000).

The species with a preference for drier microhabitats are generally located at slightly higher elevations than those with a preference for wetter microhabitats. These preferences are highlighted by their Ellenberg indicator values (EIVs) for moisture (Ellenberg et al. 1991) (Table 3.1). The EIV is a common tool in applied plant ecology in Europe (Diekmann 2003). For *Silvaum silaus*, the original indicator value for moisture after Ellenberg et al. (1991) calibrated for Central Europe is indifferent (i.e., having no preference). To be able to assign *S. silaus* to a microhabitat preference group (i.e., wet or dry), we compared the EIVs for moisture recalibrated for Great Britain (Hill et al. 1999), France (Julve 1998) and Italy (Pignatti et al. 2005). As these values were between five and seven (GB: 5, F: 7, I: 7), we interpreted this species as having a slight tendency toward wetter microhabitats and therefore assigned it to the wet microhabitat preference group to obtain a balanced experimental design. Although making use of EIVs outside their calibrated range is sometimes not recommended (Godefroid and Dana 2007), they have been widely and successfully applied across numerous areas, even outside Central Europe (Diekmann 2003). The plant species nomenclature followed Jäger (2017).

### Design and setup of experiments

To evaluate the effect of flooding depth on the response of plant performance under flooded conditions, we employed 3 depth groups: (1) partial submergence (paFl),

**Table 3.1** The 12 plant species studied in the flooding experiment (six species with a preference for either wet or dry microhabitats: wet & dry, respectively).

Species	Family	Microhabitat preference	EIV m
<i>Allium angulosum</i> L.	Alliaceae	wet	8 <sup>a</sup>
<i>Allium vineale</i> L.	Alliaceae	dry	4 <sup>a</sup>
<i>Silaum silaus</i> (L.) Schinz et Thell	Apiaceae	wet	5 <sup>b</sup> , 7 <sup>c</sup> , 7 <sup>d</sup>
<i>Pimpinella saxifraga</i> L.	Apiaceae	dry	3 <sup>a</sup>
<i>Selinum carvifolia</i> (L.) L.	Apiaceae	wet	7 <sup>a</sup>
<i>Peucedanum officinale</i> L.	Apiaceae	dry	4 <sup>a</sup>
<i>Veronica maritima</i> L.	Plantaginaceae	wet	8 <sup>a</sup>
<i>Veronica teucrium</i> L.	Plantaginaceae	dry	3 <sup>a</sup>
<i>Sanguisorba officinalis</i> L.	Rosaceae	wet	7 <sup>a</sup>
<i>Sanguisorba minor</i> Scop.	Rosaceae	dry	3 <sup>a</sup>
<i>Galium boreale</i> L.	Rubiaceae	wet	6 <sup>a</sup>
<i>Galium wirtgenii</i> F.W. Schultz	Rubiaceae	dry	4 <sup>a</sup>

EIV m, Ellenberg indicator value for moisture. Superscript letters indicate reference for EIV value: <sup>a</sup>, (Ellenberg et al. 1991); <sup>b</sup>, (Hill et al. 1999); <sup>c</sup>, (Julve 1998); <sup>d</sup>, (Pignatti et al. 2005).

flooding of plant pots to approx. 1 cm above the soil surface level, total flooding depth approx. 8 cm; (2) complete submergence (coFl), flooding depth = soil surface level + 50 cm, total flooding depth approx. 58 cm; and (3) controls with no flooding (noFl), total flooding depth 0 cm.

To analyze the effect of flooding duration, we used 2 duration groups; after 2 weeks of flooding, we removed half of the plants from the flooding treatment (2-week flooding group, 2w), and the other half remained in the flooding treatment for another 2 weeks (4-week flooding group, 4w). The combination of 12 plant species, 3 flooding depths, 2 flooding durations, and 9 replicates led to a total of 648 experimental plants.

The methodological approach of this study follows Gattringer et al. (2017): The seed material was collected from floodplain meadows along the northern Upper Rhine in Germany (UTM: 32U 455000 5523500 – 32U 462000 5518200) between August and November 2015 depending on the maturity of the seeds, or they were obtained from a producer of autochthonous seeds (Rieger-Hofmann GmbH, Blaufelden-Raboldshausen, Germany). For *Allium vineale*, reproduction via aerially produced asexual bulbils exceeds sexual reproduction (Ronsheim and Bever 2000), and thus bulbils instead of seeds were used in this experiment.

We cold-wet stratified seeds for 28 days at 4 °C in potting soil using a climate chamber (Rumed type 3401; Rubarth Apparate GmbH, Laatzen, Germany). Germination of seeds peaked after 7 days (*Veronica maritima*, *Pimpinella saxifraga*, *Sanguisorba officinalis*, *Allium angulosum*, *Galium wirtgenii*, *Selinum carvifolia*, *Veronica teucrium*, *Sanguisorba minor*) and after 11 days (*Galium boreale*, *Peucedanum officinale*, *S. silaus*), and the sprouting of bulbils (*A. vineale*; a preceding stratification procedure was skipped for bulbils) peaked after 7 days in a greenhouse (20 °C by day/15 °C by night; photoperiod: 12 hours/day). On day 14 after the germination/sprouting peak, we transplanted all seedlings (that had synchronously germinated/sprouted on one day) into pots (diameter: 9 cm on top, height: 7.8 cm) in a 1:2 ratio of sand and perlite (Knauf Aquapanel GmbH, Dortmund, Germany). We chose this substrate to allow for the minimal destruction of roots during the root washing procedure. A nutrient supply was ensured by adding slow-release Osmocote (100 g · m<sup>-2</sup>; 7.1% NO<sub>3</sub>-N, 8.9% NH<sub>4</sub>-N, 9% P<sub>2</sub>O<sub>5</sub>, 12% K<sub>2</sub>O; Osmocote Exact Standard 3-4M, Everris International B.V., Geldermalsen, The Netherlands), which represents intermediate nutrient conditions (Hidding et al. 2014)

At day 30 after the germination or sprouting of plants, 6 pots per species were randomly distributed within each of 9 outdoor ponds (positioned in 3 rows), and the flooding procedure began for all groups except the unflooded groups. Therefore, three ponds per row (i.e., block) were randomly assigned to a flooding depth group. The ponds consisted of wooden boxes lined with white silage foil (length: 1 m; width 1 m; height: 0.6 m) and were located outside on a paved area under unshaded conditions (Giessen, Germany, UTM: 32U 478260 5598300). Before the start of the flooding procedure, we measured the total plant height of all experimental plants. Three days after the end of each flooding procedure, we quantified the other variables. Total plant height was measured from the soil surface to the longest shoot of the plant. The roots were washed, and the length of the longest root was measured. For the calculation of specific leaf area (SLA), we scanned three fully expanded, average-sized leaves from every plant and measured the size using the R package *EImage* (Pau et al. 2010). The biomass of the shoots and roots and three leaves for determination of SLA were dried (48 hours at 60 °C) and weighed. We calculated the SLA as the leaf area per kg of leaf dry mass (m<sup>2</sup> · kg<sup>-1</sup>) (Poorter et al. 2012) and the root mass fraction (RMF) as the root dry mass per g of total plant dry mass (g · g<sup>-1</sup>) (Poorter et al. 2012). The experiment was performed from March to June 2016.

## Analysis

Before the analyses, plant height, root length, aboveground biomass, belowground biomass, and total biomass were standardized using the natural logarithmic response ratio ( $RR$ ) as suggested by Goldberg and Scheiner (2001):

$$RR = \ln(P_T/\overline{P_C})$$

The  $RR$  was calculated as the ratio of the treated sample ( $P_T$ ) to the mean value of the unflooded group (i.e., control;  $\overline{P_C}$ ) for each species for each flooding duration combination. This standardization allows comparisons across species and flooding duration groups. As the RMF and SLA already represent ratios, we skipped the  $RR$  procedure for these variables. For analyses with these response variables, we excluded individuals for which ratio calculation was not possible (i.e., division by zero; RMF: 2 individuals) or the SLA was not measureable (i.e., leaf area below the detection limit for the scanning procedure; SLA: 73 individuals). All other response variables were calculable for all plants ( $n = 648$ ).

In the first step, we calculated one-way ANOVAs with the factor plant family for every response variable, as different subsets of species were nested within each family and each microhabitat (species pairs from the same family (often genus) were selected owing to their morphological similarity but difference in microhabitat preference). Thus, the factors microhabitat preference and family could not be incorporated in the same statistical model. This study mainly focuses on determining the response of species with different microhabitat preferences to different flooding depths and flooding durations. Therefore, we accounted for the inherent effects of family identity by computing these one-way ANOVAs ( $RR$  of plant height:  $F = 8.9$ ,  $p < 0.001$ ;  $RR$  of root length:  $F = 12.1$ ,  $p < 0.001$ ;  $RR$  of aboveground biomass:  $F = 18.4$ ,  $p < 0.001$ ;  $RR$  of belowground biomass:  $F = 15.9$ ,  $p < 0.001$ ;  $RR$  of total biomass:  $F = 16.2$ ,  $p < 0.001$ ; RMF:  $F = 56.0$ ,  $p < 0.001$ ; SLA:  $F = 12.4$ ,  $p < 0.001$ ). We used the residuals of these ANOVAs for the subsequent analyses.

Second, we computed multifactorial ANCOVAs for each response variable including the main effects and all interactions of the factors flooding duration, flooding depth, species (nested within microhabitat preference), and microhabitat preference and the main effect of the covariate  $RR$  of initial height (i.e., the total plant height before the flooding procedure began). By including this covariate in the analyses, we accounted for differences in plant individuals at the beginning of the experiment, which may reduce unexplained variation and increase the statistical power of the tests (Quinn and Keough 2002). The random factor block was excluded from the analyses after we had checked using ANCOVAs that it only explained a negligible

amount of the total variance and almost did not affect the significance of the main effects and interactions (Newman et al. 1997) (Annex 3 Table 3.A1). For pairwise comparisons, we conducted post hoc Tukey’s HSD tests. We visually checked requirements to conduct ANOVA/ANCOVA analyses (e.g., normality) by using diagnostic plots. We used the ratio of the sum of squares of a factor/interaction to the total sum of squares to obtain the relative contribution of each factor or interaction to the total variance. The significance threshold was set at 0.05. All statistical analyses and data visualizations were performed using R 3.4.1 (R Core Team 2017) and ggplot2 2.2.1 (Wickham 2009).

## Results

All response variables were significantly affected by the interaction of flooding depth and flooding duration (Table 3.2). With increasing flooding depth, the effect of flooding duration was even more detrimental than that resulting from the addition of the two individual effects (Fig. 3.1a). The total biomass of *S. carvifolia*, *P. saxifraga*, *Veronica* species, *Sanguisorba* species, and *Galium* species dropped dramatically under 4 weeks of flooding compared to that under 2 weeks of flooding with increasing depth (Fig. 3.2b, note the logarithmic scale). This duration-depth effect was species specific (i.e., species (nested within microhabitat preference)  $\times$  flooding depth  $\times$  flooding duration interaction); for several species, a considerable reduction in total biomass – and for some species, a shift in RMF and SLA – was already observed at lower levels of the combined effect (e.g., for *P. saxifraga* at partial/4 weeks and *V. teucrium* at partial/2 weeks), while other species showed such a change only at high combination levels (e.g., *S. carvifolia* at complete/4 weeks and *V. maritima* at complete/4 weeks; Fig. 3.2b-d).

Species from drier microhabitats seemed to be more susceptible to flooding effects on their performance than species from wetter microhabitats, especially in the 4-week and partial flooding groups (Fig. 3.1b-c; Fig. 3.2). Plants with a preference for wet microhabitats showed higher biomass, longer root length and higher SLA than plants from dry microhabitats (Table 3.2).

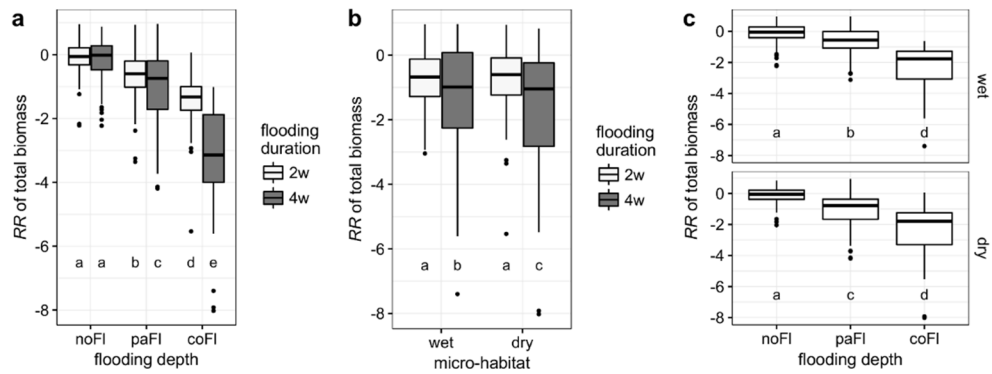
**Table 3.2** ANCOVA results for 12 floodplain meadow plant species in the flooding experiment.

	Total plant height				Root length				Aboveground biomass				Belowground biomass			
	df	F	sig	vc	df	F	sig	vc	df	F	sig	vc	df	F	sig	vc
Microhabitat preference (MH)	1	0.7	ns	0.1	1	24.4	***	2.2	1	6.9	**	0.3	1	9.5	**	0.4
Flooding depth (DE)	2	101.0	***	15.0	2	73.9	***	13.4	2	422.2	***	34.8	2	621.9	***	49.7
Flooding duration (DU)	1	60.9	***	4.5	1	30.5	***	2.8	1	205.4	***	8.5	1	110.7	***	4.4
Species (MH) [S (MH)]	10	4.9	***	3.6	10	6.9	***	6.3	10	6.8	***	2.8	10	7.2	***	2.9
MH × DE	2	3.5	*	0.5	2	10.0	***	1.8	2	5.9	**	0.5	2	18.8	***	1.5
MH × DU	1	0.1	ns	0.0	1	10.0	**	0.9	1	6.9	**	0.3	1	11.3	***	0.5
DE × DU	2	49.9	***	7.4	2	8.6	***	1.6	2	119.8	***	9.9	2	36.8	***	2.9
S (MH) × DE	20	6.4	***	9.5	20	5.3	***	9.7	20	12.4	***	10.2	20	10.2	***	8.2
S (MH) × DU	10	6.2	***	4.6	10	4.8	***	4.4	10	6.6	***	2.7	10	6.1	***	2.4
MH × DE × DU	2	1.0	ns	0.1	2	3.3	*	0.6	2	1.4	ns	0.1	2	5.0	**	0.4
S (MH) × DE × DU	20	6.3	***	9.3	20	2.3	**	4.1	20	5.6	***	4.6	20	4.1	***	3.3
Covariate: initial height	1	37.3	***	2.8	1	0.0	ns	0.0	1	37.0	***	1.5	1	10.8	**	0.4
Residuals	575			42.6	575			52.2	575			23.7	575			23.0

	Total biomass				Root mass fraction (RMF)				Specific leaf area (SLA)			
	df	F	sig	vc	df	F	sig	vc	df	F	sig	vc
Microhabitat preference (MH)	1	7.0	**	0.3	1	0.2	ns	0.0	1	52.5	***	5.2
Flooding depth (DE)	2	589.9	***	45.8	2	44.9	***	6.9	2	46.7	***	9.2
Flooding duration (DU)	1	189.0	***	7.3	1	97.3	***	7.4	1	42.9	***	4.2
Species (MH) [S (MH)]	10	5.2	***	2.0	10	6.0	***	4.6	10	9.6	***	9.4
MH × DE	2	9.4	***	0.7	2	2.0	ns	0.3	2	4.9	**	1.0
MH × DU	1	8.0	**	0.3	1	0.2	ns	0.0	1	0.2	ns	0.0
DE × DU	2	98.1	***	7.6	2	41.5	***	6.3	2	3.5	*	0.7
S (MH) × DE	20	9.1	***	7.1	20	12.9	***	19.8	20	8.8	***	17.3
S (MH) × DU	10	5.7	***	2.2	10	2.3	*	1.8	10	0.5	ns	0.5
MH × DE × DU	2	2.4	.	0.2	2	1.0	ns	0.2	2	0.0	ns	0.0
S (MH) × DE × DU	20	3.9	***	3.0	20	5.3	***	8.1	16	1.2	ns	1.9
Covariate: initial height	1	30.3	***	1.2	1	10.2	**	0.8	1	8.2	**	0.8
Residuals	575			22.3	573			43.8	506			49.8

The effects of the factors microhabitat preference, species (nested within microhabitat preference), flooding duration, and flooding depth on the logarithmic response ratio (*RR*) of total plant height, *RR* of root length, *RR* of aboveground biomass, *RR* of belowground biomass, *RR* of total biomass, root mass fraction (RMF), and specific leaf area (SLA) of experimental plant individuals were tested using ANCOVA with the covariate *RR* of height of plants at the beginning of the flooding procedure.

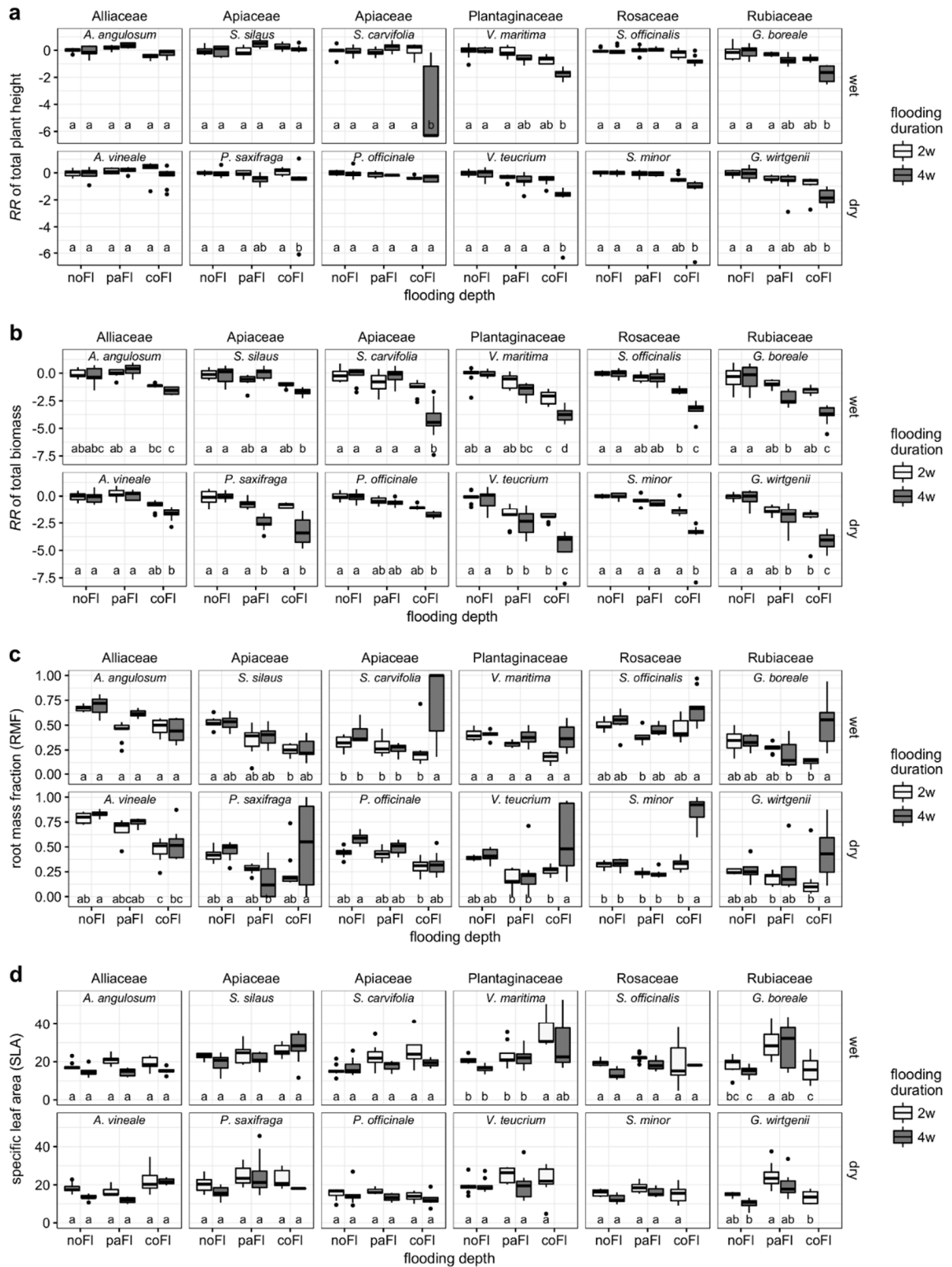
df, degrees of freedom; F, variance ratio; sig, significance levels of error probability ( $p < 0.001 = \text{***}$ ,  $p < 0.01 = \text{**}$ ,  $p < 0.05 = *$ ,  $p < 0.1 = .$ ,  $p > 0.1 = \text{ns}$ ); vc (%), relative contribution of individual factors and their interactions to total variance.



**Fig. 3.1** Two-way-interaction boxplots of the logarithmic response ratio ( $RR$ ) of total biomass at the end of the flooding experiment: 12 plant species (six species with a preference for either wet or dry microhabitats: wet & dry, respectively) under a flooding duration of 2 and 4 weeks (2w & 4w) and in flooding depth groups of no flooding (i.e., control), partial flooding, and complete flooding (noFl, paFl, coFl). Flooding depth  $\times$  flooding duration interaction (**a**); microhabitat preference  $\times$  flooding duration interaction (**b**); flooding depth  $\times$  microhabitat preference interaction (**c**). Different letters denote significantly different groups (post hoc Tukey's HSD tests,  $p < 0.05$ ); boxes represent the 25th and 75th percentiles and the median value (line); whiskers indicate 1.5 times the interquartile range (or the largest/smallest value in the data if it is lower than 1.5 IQR); points represent outlying data beyond the whiskers.

Flooding depth significantly affected plant performance for all response variables and explained large amounts of the total variance for several response variables in the ANCOVA analyses (Table 3.2). Further, the effect of flooding depth was species specific, as indicated by the species (nested within microhabitat preference)  $\times$  flooding depth interaction (Table 3.2). The RMF, total biomass and plant height of several species were more reduced after complete compared to partial flooding (Fig. 3.2a-c). Furthermore, *A. angulosum*, *S. silaus*, and *S. carvifolia* showed a slightly higher (though not significantly different; Tukey's HSD test:  $p > 0.9$ ) plant height under partial flooding compared to non-flooded conditions (Fig. 3.2a; original data in Annex 3 Fig. 3.A2a). Under complete flooding, this effect vanished, and the plants reacted with decreased performance.

The factor flooding duration also explained part of the variation in plant performance and proved to be species specific (Table 3.2). An additional two weeks of flooding led to a significant decrease in height and biomass (Fig. 3.1) as well as shifts in the RMF and SLA of plants. The higher SLA values in our experiment were mostly a result of thinner leaves, as leaf biomass decreased more than leaf area in most species.



**Fig. 3.2** Boxplots of the logarithmic response ratio ( $RR$ ) of total plant height (a),  $RR$  of total biomass (b), root mass fraction (RMF; c), and specific leaf area (SLA; d) at the end of the flooding experiment: 12 plant species (six species with a preference for either wet or dry microhabitats: wet & dry, respectively) under a flooding duration of 2 and 4 weeks (2w & 4w) and in flooding depth groups of no flooding (i.e., control), partial flooding, and complete



flooding (noFl, paFl, coFl). Different letters denote significantly different groups (post hoc Tukey's HSD tests,  $p < 0.05$ ) within each species; boxes represent the 25th and 75th percentiles and the median value (line); whiskers indicate 1.5 times the interquartile range (or the largest/smallest value in the data if it is lower than 1.5 IQR); points represent outlying data beyond the whiskers. Missing boxes in (d) represent groups for which the SLA was not measurable (i.e., below the limit of detection).

A general trend independent of the flooding procedure was observed for SLA: older plants from the 4-week group showed lower SLA values than plants from the 2-week group (i.e., thicker leaves, as leaf weight increases more than leaf area). Some individuals suffered considerable losses of aboveground biomass under 4 weeks of flooding, and hence the SLA could also not be detected for some individuals (Fig. 3.2).

## Discussion

### Combination of flooding depth and duration

Our experiment revealed the importance of the combined effect of flooding duration and depth on the performance of species during submergence (Table 3.2). Further, the results imply non-additive (i.e., interactive) effects for this combination, and we can thus accept our first hypothesis. This finding is in line with Vervuren et al. (2003), who note that the impact of floods is determined by the interplay among several components of a flood. Although several other factors might influence the impacts of flooding on plants, the two determinants depth and duration are among the key flooding regime factors determining the flooding tolerance of species (Cronk and Fennessy 2001; Vervuren et al. 2003; Magee and Kentula 2005). Accordingly, the species' sensitivity to the combination of flooding depth and duration plays a crucial role in their capacity to establish in floodplain grassland.

In floodplain meadow species, the flooding tolerance of a species seems to be linked with the ability of the species to cope with the depth  $\times$  duration interaction effect (i.e., intensity of the flooding treatment). For the experimental flooding groups, this effect could be sorted from low to high as (1) partial/2 weeks, (2) partial/4 weeks, (3) complete/2 weeks, and (4) complete/4 weeks (Fig. 3.1a). For several of the experimental species, our results might suggest the existence of a tipping point in terms of the depth-duration combination at which plants can no longer cope with the stress through their usual adaptation cascade and suffer severe damage. Indications of such tipping points were observable, for instance, for the response variables total

plant height and biomass (although not always significant; Fig. 3.2a-b); for example, *S. carvifolia* and *Galium* species showed a considerable decrease in height and biomass between the complete/2-week and complete/4-week groups, *Allium* species showed a substantial decrease in biomass between the partial/4-week and complete/2-week groups, and *P. saxifraga* showed a decrease in biomass in the partial/4-week and complete/4-week groups. Some species were more vulnerable to deterioration through depth effects (e.g., *V. maritima*; Fig. 3.2b), while others were more vulnerable via duration effects (e.g., *P. saxifraga*; Fig. 3.2b). For several species, these patterns also seemed to persist in other response variables (e.g., *Galium* species for the RMF and SLA; Fig. 3.2c-d). In addition, Blom et al. (1994) found species specific thresholds in eight floodplain grassland species after which flooding effects become detrimental. In contrast, for some response variables and some species, tipping points were not visible (e.g., *S. silaus* for the total height, RMF, and SLA; *V. maritima* for the RMF; *P. officinale* for the total height and RMF; Fig. 3.2). In these cases, our treatment may not have exerted enough stress on the plants. Therefore, to demonstrate the existence of such thresholds in the effect of the depth  $\times$  duration interaction on riparian species, an experimental design with finer scaling of the depth and duration gradients would be necessary.

### **Microhabitat preference**

We found evidence that flood-sensitive species with a preference for drier microhabitats show limited performance under flooding compared to species from wet microhabitats (Fig. 3.2). This result corresponds with those from several previous studies; for example, under flooded conditions, floodplain meadow species preferring wet microhabitats survived longer and grew taller than species from dry microhabitats (Jung et al. 2008; Gattringer et al. 2017). Moreover, our results show that the differences in the flooding tolerance of species with differing microhabitat preferences are determined by the factors duration and depth. In terms of flooding duration, the microhabitat preference groups responded differently only under the 4-week-flooding treatment (Fig. 3.1b). Regarding flooding depth, partial flooding resulted in different outcomes in the microhabitat preference groups, whereas complete flooding did not show such an effect (Fig. 3.1c). Thus, we can partly accept our second hypothesis that flooded plants with a preference for wet microhabitats show better performance than those with a preference for dry microhabitats. Nevertheless, it seems clear that hydrological niche segregation exists – not only on coarse and fine scales in floodplain meadows (Silvertown et al. 1999) but also in numerous other ecosystems (for a review, see Silvertown et al. 2015). In general, water availability locally influences the

distribution and composition of vegetation. Accordingly, plant niches can be attributed to species specific ranges of soil water conditions (Silvertown et al. 2015). However, Silvertown et al. (2015) also mentioned that plants might be phenotypically plastic under stresses, such as flooding events, which could explain the evidence regarding microhabitat preference found in this study.

### **Flooding depth**

As expected, the effects of flooding on the performance of plants were more severe under complete submergence than under partial flooding. These results agree with the previous findings of Vervuren et al. (2003), in which the survival of riparian grassland species decreased with an increase in flooding depth. In several species, we found that plant performance was more reduced after complete flooding in comparison to partial flooding (Fig. 3.2a-c). This reaction is partly in line with the findings of Mauchamp et al. (2001): juveniles of *Phragmites australis* showed largely diminished biomass production and growth under complete submergence but also enhanced performance under a partial submergence treatment. These patterns have been described as “low-oxygen quiescence syndrome” when plants respond with the protection of meristem or organs (i.e., diminished biomass production) and “low-oxygen escape syndrome” when plants try to escape submergence (i.e., elongated shoots) (Voesenek and Bailey-Serres 2013). Likewise, our findings of suppressed elongation and a reduced RMF under complete submergence indicate a quiescence strategy. This was also true of most of the species with a preference for drier microhabitats under the partial flooding treatment (Fig. 3.2a). Interestingly, some species from wet microhabitats (*A. angulosum*, *S. silaus*, and *S. carvifolia*) showed slight (though not significant) elongation (Fig. 3.2a; Annex 3 Fig. 3.A2a), which could be interpreted as an escape strategy under partial submergence but a quiescence strategy under the complete submergence treatment. Similarly, Manzur et al. (2009) detected that *Lotus tenuis* switches strategies depending on flooding depth. Further, they suggested that the documented ability to change survival strategies could explain the success of species in environments facing unpredictable floodwater depths. Transferring this to the floodplain meadow species in our experiment strongly highlights their suitable adaptation to cope with regular flooding. Hence, this evidence also emphasizes their ability to outcompete flood-sensitive (mostly ubiquitous) species.

### **Flooding duration**

An increased flooding duration (2 weeks vs. 4 weeks) had increasingly detrimental effects on plants and their performance, as expected. This result is in accordance with

findings for numerous floodplain grassland species (Blom et al. 1994; Van Eck et al. 2004). However, the decrease in biomass and the RMF from 2 weeks to 4 weeks may partly reflect the dying of root tissue (Poorter et al. 2012). Other experiments have shown that root tissue dies rather fast under submergence, which might lead to biomass losses through reduced nutrient uptake (Visser et al. 2016). Webb et al. (2012) indicated that an increase in flooding duration does not increase the establishment of wetland plant species (i.e., mainly plants from semi-aquatic habitats, such as *Phragmites australis* and *Phalaris arundinacea*). However, our results clearly demonstrate that flooding duration plays an important role in the response of floodplain meadow species to a flooding event. The fact that the 4-week group (which was 2 weeks older at harvest than the 2-week group) showed lower SLA values in this experiment (particularly for the no-flooding group; Fig. 3.2d) is in line with previous findings of decreased SLA with increasing plant age (Reich et al. 1991; Milla et al. 2008). Some plant individuals in the 4-week flooding treatment showed a considerable loss of aboveground biomass. In this case, the flooding procedure had a strong effect on plants (e.g., on Apiaceae species, such as *S. carvifolia* and *P. saxifraga* under complete flooding) that were partially still in the rosette stadium (Eriksson and Ehrlén 2008)). Therefore, in those individuals, the SLA could usually not be determined, as leaf size was below the limit of detection for the scanning procedure (Poorter et al. 2012).

## Conclusions

We conclude that increases in flooding depth, flooding duration, and the combination of the two factors result in severe limitations to seedling establishment. Based on our results, we think that the interactive effect of flooding depth and duration on the flooding tolerance of species has been underestimated in plant ecological experiments. Although numerous (experimental) studies have focused on the effects of flooding on plants (e.g., Webb et al. 2012), their results are often difficult to compare or evaluate if only one key determinant (such as flooding duration only) was taken into account. In future studies, other flooding components (e.g., flooding frequency or floodwater temperature) could be combined with flooding depth and duration to further understand plant responses to flooding events.

## Acknowledgements

We thank Josef Scholz-vom Hofe, Madeleine Seip, and Tatjana Kage for assistance in growing the plants and data collection. This study was funded by the Deutsche Bundesstiftung Umwelt (DBU; Project-No. 31612/01; [www.dbu.de](http://www.dbu.de)). We thank two anonymous reviewers for their valuable comments, which helped us to improve this manuscript.

## Conflict of Interest

The authors declare that they have no conflict of interest.

## References

- Bailey-Serres J, Voesenek LACJ (2008) Flooding Stress: Acclimations and Genetic Diversity. *Annu Rev Plant Biol* 59:313–339. doi: 10.1146/annurev.arplant.59.032607.092752
- Blom CWPM, Voesenek LACJ, Banga M, Engelaar WMHG, Rijnders JHGM, Van De Steeg HM, Visser EJW (1994) Physiological Ecology of Riverside Species: Adaptive Responses of Plants to Submergence. *Ann Bot* 74:253–263. doi: 10.1006/anbo.1994.1116
- Burkart M (2001) River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. *Glob Ecol Biogeogr* 10:449–468. doi: 10.1046/j.1466-822x.2001.00270.x
- Burkart M, Dierschke H, Hölzel N, Nowak B, Fartmann T (2004) Molinio-Arrhenatheretea (E1) - Kulturgrasland und verwandte Vegetationstypen (Molinio-Arrhenatheretea E1 - Cultural grassland and related vegetation types). *Synop Pflanzengesellschaften Dtschl* 1–103
- Byun C, Nam JM, Kim JG (2017) Effects of flooding regime on wetland plant growth and species dominance in a mesocosm experiment. *Plant Ecol* 218:517–527. doi: 10.1007/s11258-017-0707-0
- Cronk JK, Fennessy MS (2001) *Wetland Plants: Biology and Ecology*. CRC Press, Boca Raton, FL
- Diekmann M (2003) Species indicator values as an important tool in applied plant ecology – a review. *Basic Appl Ecol* 4:493–506. doi: 10.1078/1439-1791-00185
- Donath TW, Bissels S, Hölzel N, Otte A (2007) Large scale application of diaspore transfer with plant material in restoration practice – Impact of seed and microsite limitation. *Biol Conserv* 138:224–234. doi: 10.1016/j.biocon.2007.04.020
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1991) *Zeigerwerte von Pflanzen in Mitteleuropa (Indicator values of plants in Central Europe)*, 3rd edn. Goltze, Göttingen

- Engst K, Baasch A, Erfmeier A, Jandt U, May K, Schmiede R, Bruelheide H (2016) Functional community ecology meets restoration ecology: Assessing the restoration success of alluvial floodplain meadows with functional traits. *J Appl Ecol* 53:751–764. doi: 10.1111/1365-2664.12623
- Eriksson O, Ehrlén J (2008) Seedling recruitment and population ecology. In: Leck MA, Parker VT, Simpson R (eds) *Seedling Ecology and Evolution*. Cambridge University Press, Cambridge
- Finck P, Heinze S, Raths U, Riecken U, Ssymank A (2017) Rote Liste der gefährdeten Biotoptypen Deutschlands. Dritte fortgeschriebene Fassung (Red list of threatened habitat types in Germany. Third updated version). *Naturschutz Biol Vielfalt* 156:1–460
- Gattringer JP, Donath TW, Eckstein RL, Ludewig K, Otte A, Harvolk-Schöning S (2017) Flooding tolerance of four floodplain meadow species depends on age. *PLoS ONE* 12:e0176869. doi: 10.1371/journal.pone.0176869
- Gitzendanner MA, Soltis PS (2000) Patterns of genetic variation in rare and widespread plant congeners. *Am J Bot* 87:783–792. doi: 10.2307/2656886
- Godefroid S, Dana ED (2007) Can Ellenberg's indicator values for Mediterranean plants be used outside their region of definition? *J Biogeogr* 34:62–68. doi: 10.1111/j.1365-2699.2006.01582.x
- Goldberg DE, Scheiner SM (2001) ANOVA and ANCOVA: field competition experiments. In: Scheiner SM, Gurevitch J (eds) *Design and Analysis of Ecological Experiments*, 2nd edn. Oxford University Press, Oxford, New York, pp 77–98
- Groom MJ, Meffe GK, Carroll CR (2006) *Principles of Conservation Biology*, 3rd edn. Sinauer Associates, Inc., Sunderland
- Hidding B, Sarneel JM, Bakker ES (2014) Flooding tolerance and horizontal expansion of wetland plants: Facilitation by floating mats? *Aquat Bot* 113:83–89. doi: 10.1016/j.aquabot.2013.11.003
- Hill MO, Mountford JO, Roy DB, Bunce RGH (1999) *Ellenberg's Indicator Values for British Plants*. ECOFACT Volume 2 Technical Annex. Institute of Terrestrial Ecology, Huntingdon
- Hölzel N, Otte A (2004) Inter-annual variation in the soil seed bank of flood-meadows over two years with different flooding patterns. *Plant Ecol* 174:279–291. doi: 10.1023/B:VEGE.0000049108.04955.e2
- Jäger EJ (ed) (2017) *Rothmaler - Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband (Fieldflora of Germany, vascular plants, basic volume)*, 21st edn. Springer Spektrum, Berlin
- Joyce CB, Wade PM (1998) Wet Grasslands: A European Perspective. In: Joyce CB, Wade PM (eds) *European Wet Grasslands: Biodiversity, Management and Restoration*. Wiley, Chichester, UK, pp 1–12
- Julve P (1998) *Baseflor. Index botanique, écologique et chorologique de la flore de France (Botanical, ecological and chorological index of the flora of France)*. Version: 23 mai 2017. philippe.julve.pagesperso-orange.fr/catminat.htm. Accessed 23 May 2017

- Jung V, Hoffmann L, Muller S (2008) Ecophysiological responses of nine floodplain meadow species to changing hydrological conditions. *Plant Ecol* 201:589–598. doi: 10.1007/s11258-008-9508-9
- Ludewig K, Zelle B, Eckstein RL, Mosner E, Otte A, Donath TW (2014) Differential effects of reduced water potential on the germination of floodplain grassland species indicative of wet and dry habitats. *Seed Sci Res* 24:49–61. doi: 10.1017/S096025851300038X
- Madsen TV, Sand-Jensen K (1994) The interactive effects of light and inorganic carbon on aquatic plant growth. *Plant Cell Environ* 17:955–962. doi: 10.1111/j.1365-3040.1994.tb00324.x
- Magee TK, Kentula ME (2005) Response of wetland plant species to hydrologic conditions. *Wetl Ecol Manag* 13:163–181. doi: 10.1007/s11273-004-6258-x
- Malanson GP (1993) *Riparian Landscapes*. Cambridge University Press, Cambridge
- Manzur ME, Grimoldi AA, Insausti P, Striker GG (2009) Escape from water or remain quiescent? *Lotus tenuis* changes its strategy depending on depth of submergence. *Ann Bot* 104:1163–1169. doi: 10.1093/aob/mcp203
- Mathar W, Kleinebecker T, Hölzel N (2015) Environmental variation as a key process of co-existence in flood-meadows. *J Veg Sci* 26:480–491. doi: 10.1111/jvs.12254
- Mauchamp A, Blanch S, Grillas P (2001) Effects of submergence on the growth of *Phragmites australis* seedlings. *Aquat Bot* 69:147–164. doi: 10.1016/S0304-3770(01)00135-8
- Milla R, Reich PB, Niinemets Ü, Castro-Díez P (2008) Environmental and developmental controls on specific leaf area are little modified by leaf allometry. *Funct Ecol* 22:565–576. doi: 10.1111/j.1365-2435.2008.01406.x
- Newman JA, Bergelson J, Grafen A (1997) Blocking factors and hypothesis tests in ecology: is your statistics text wrong? *Ecology* 78:1312–1320. doi: 10.1890/0012-9658(1997)078[1312:BFAHTI]2.0.CO;2
- Nicol JM, Ganf GG, Walker KF, Gawne B (2018) Response of three arid zone floodplain plant species to inundation. *Plant Ecol* 219:57–67. doi: 10.1007/s11258-017-0777-z
- Pau G, Fuchs F, Sklyar O, Boutros M, Huber W (2010) EBIImage—an R package for image processing with applications to cellular phenotypes. *Bioinformatics* 26:979–981. doi: 10.1093/bioinformatics/btq046
- Pignatti S, Menegoni P, Pietrosanti S (2005) Biondicazione attraverso le piante vascolari. Valori di indicazione secondo Ellenberg (Zeigerwerte) per le specie della Flora d'Italy (Bioindication through vascular plants. Indicator values according to Ellenberg for species of the flora of Italy). *Braun-Blanquetia* 39:1–97
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* 193:30–50. doi: 10.1111/j.1469-8137.2011.03952.x
- Quinn GP, Keough MJ (2002) *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, New York

- R Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria
- Reich PB, Walters MB, Ellsworth DS (1991) Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area and photosynthesis in maple and oak trees. *Plant Cell Environ* 14:251–259. doi: 10.1111/j.1365-3040.1991.tb01499.x
- Ronsheim ML, Bever JD (2000) Genetic Variation and Evolutionary Trade-Offs for Sexual and Asexual Reproductive Modes in *Allium vineale* (Liliaceae). *Am J Bot* 87:1769–1777. doi: 10.2307/2656827
- Silvertown J, Araya Y, Gowing D (2015) Hydrological niches in terrestrial plant communities: a review. *J Ecol* 103:93–108. doi: 10.1111/1365-2745.12332
- Silvertown J, Dodd ME, Gowing DJG, Mountford JO (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. *Nature* 400:61–63. doi: 10.1038/21877
- Tockner K, Stanford JA (2002) Riverine flood plains: present state and future trends. *Environ Conserv* 29:308–330. doi: 10.1017/S037689290200022X
- Van Eck WHJM, Lenssen JPM, Rengelink RHJ, Blom CWPM, De Kroon H (2005) Water temperature instead of acclimation stage and oxygen concentration determines responses to winter floods. *Aquat Bot* 81:253–264. doi: 10.1016/j.aquabot.2004.10.006
- Van Eck WHJM, Van De Steeg HM, Blom CWPM, 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. doi: 10.1111/j.0030-1299.2004.13083.x
- Vervuren PJA, Blom CWPM, De Kroon H (2003) Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. *J Ecol* 91:135–146. doi: 10.1046/j.1365-2745.2003.00749.x
- Visser EJW, Zhang Q, De Gruyter F, Martens S, Huber H (2016) Shade affects responses to drought and flooding – acclimation to multiple stresses in bittersweet (*Solanum dulcamara* L.). *Plant Biol* 18:112–119. doi: 10.1111/plb.12304
- Voesenek LACJ, Bailey-Serres J (2013) Flooding tolerance: O<sub>2</sub> sensing and survival strategies. *Curr Opin Plant Biol* 16:647–653. doi: 10.1016/j.pbi.2013.06.008
- Webb JA, Wallis EM, Stewardson MJ (2012) A systematic review of published evidence linking wetland plants to water regime components. *Aquat Bot* 103:1–14. doi: 10.1016/j.aquabot.2012.06.003
- Wickham H (2009) *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York



## Annex 3

**Table 3.A1** ANCOVA results (including the random factor block) for 12 floodplain meadow plant species in the flooding experiment.

	Total plant height				Root length				Aboveground biomass				Belowground biomass			
	df	F	sig	vc	df	F	sig	vc	df	F	sig	vc	df	F	sig	vc
Microhabitat preference (MH)	1	0.7	ns	0.1	1	25.0	***	2.2	1	7.1	**	0.3	1	9.8	**	0.4
Flooding depth (DE)	2	101.6	***	15.0	2	75.6	***	13.4	2	432.9	***	34.8	2	639.2	***	49.7
Flooding duration (DU)	1	61.2	***	4.5	1	31.2	***	2.8	1	210.6	***	8.5	1	113.8	***	4.4
Species (MH) [S (MH)]	10	4.9	***	3.6	10	7.1	***	6.3	10	7.0	***	2.8	10	7.4	***	2.9
MH × DE	2	3.6	*	0.5	2	10.3	***	1.8	2	6.1	**	0.5	2	19.4	***	1.5
MH × DU	1	0.1	ns	0.0	1	10.2	**	0.9	1	7.1	**	0.3	1	11.6	***	0.5
DE × DU	2	50.2	***	7.4	2	8.8	***	1.6	2	122.8	***	9.9	2	37.8	***	2.9
S (MH) × DE	20	6.4	***	9.5	20	5.5	***	9.7	20	12.7	***	10.2	20	10.5	***	8.2
S (MH) × DU	10	6.2	***	4.6	10	4.9	***	4.4	10	6.7	***	2.7	10	6.3	***	2.4
MH × DE × DU	2	1.0	ns	0.1	2	3.4	*	0.6	2	1.5	ns	0.1	2	5.2	**	0.4
S (MH) × DE × DU	20	6.3	***	9.3	20	2.3	***	4.1	20	5.8	***	4.6	20	4.2	***	3.3
Covariate: initial height	1	38.4	***	2.8	1	0.1	ns	0.0	1	37.8	***	1.5	1	11.7	***	0.5
Block: initial height	1			0.0	1			0.4	1			0.0	1			0.0
Block: residuals	1			0.3	1			0.9	1			0.7	1			0.6
Residuals	573			42.2	573			50.9	573			23.1	573			22.3

The effects of the factors microhabitat preference, species (nested within microhabitat preference), flooding duration, and flooding depth on the logarithmic response ratio ( $RR$ ) of total plant height,  $RR$  of root length,  $RR$  of aboveground biomass,  $RR$  of belowground biomass,  $RR$  of total biomass, root mass fraction (RMF), and specific leaf area (SLA) of experimental plant individuals were tested using ANCOVA with the covariate  $RR$  of height of plants at the beginning of the flooding procedure. In addition, the random effect for block was included to account for possible effects of position of 9 ponds within 3 rows. This analysis proved that the block (i.e., rows) only explained a very small amount of total variance. Hence, we excluded this factor for further analyses.

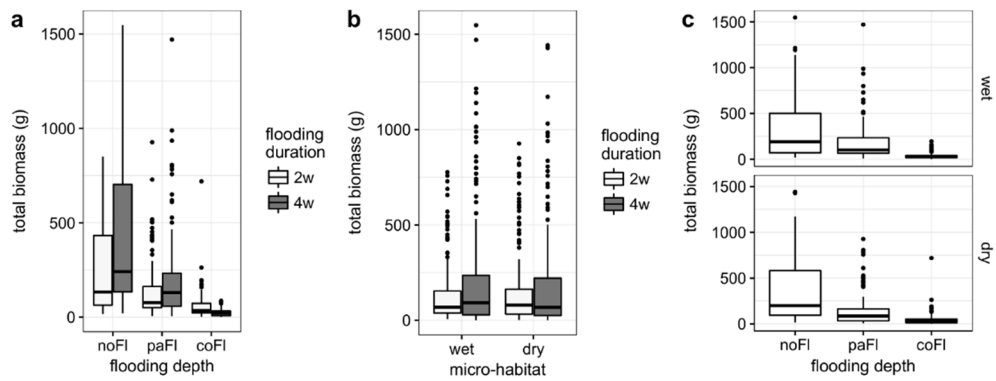
df, degrees of freedom; F, variance ratio; sig, significance levels of error probability ( $p < 0.001 = ***$ ,  $p < 0.01 = **$ ,  $p < 0.05 = *$ ,  $p < 0.1 = .$ ,  $p > 0.1 = ns$ ); vc (%), relative contribution of individual factors and their interactions to total variance.

**Table 3.A1** continued

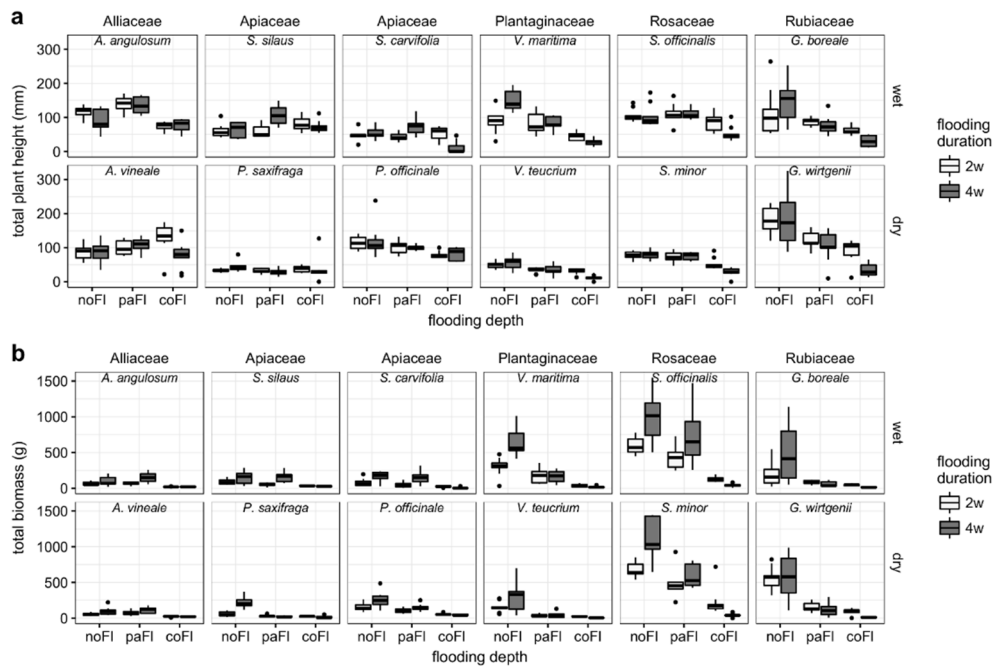
	Total biomass				Root mass fraction (RMF)				Specific leaf area (SLA)			
	df	F	sig	vc	df	F	sig	vc	df	F	sig	vc
Microhabitat preference (MH)	1	7.3	**	0.3	1	0.2	ns	0.0	1	53.3	***	5.1
Flooding depth (DE)	2	610.9	***	45.8	2	44.8	***	6.9	2	48.5	***	9.2
Flooding duration (DU)	1	195.7	***	7.3	1	97.1	***	7.4	1	44.9	***	4.3
Species (MH) [S (MH)]	10	5.4	***	2.0	10	6.0	***	4.6	10	9.9	***	9.4
MH × DE	2	9.7	***	0.7	2	2.0	ns	0.3	2	4.8	**	0.9
MH × DU	1	8.3	**	0.3	1	0.2	ns	0.0	1	0.3	ns	0.0
DE × DU	2	101.6	***	7.6	2	41.4	***	6.3	2	3.4	*	0.7
S (MH) × DE	20	9.4	***	7.1	20	12.9	***	19.8	20	9.1	***	17.3
S (MH) × DU	10	5.9	***	2.2	10	2.3	*	1.8	10	0.6	ns	0.5
MH × DE × DU	2	2.5	.	0.2	2	1.0	ns	0.2	2	0.0	ns	0.0
S (MH) × DE × DU	20	4.0	***	3.0	20	5.3	***	8.1	16	1.2	ns	1.8
Covariate: initial height	1	31.6	***	1.2	1	9.9	**	0.8	1	7.0	**	0.7
Block: initial height	1			0.0	1			0.0	1			0.9
Block: residuals	1			0.8	1			0.0	1			1.5
Residuals		573		21.5		571		43.8		504		47.8

The effects of the factors microhabitat preference, species (nested within microhabitat preference), flooding duration, and flooding depth on the logarithmic response ratio ( $RR$ ) of total plant height,  $RR$  of root length,  $RR$  of aboveground biomass,  $RR$  of belowground biomass,  $RR$  of total biomass, root mass fraction (RMF), and specific leaf area (SLA) of experimental plant individuals were tested using ANCOVA with the covariate  $RR$  of height of plants at the beginning of the flooding procedure. In addition, the random effect for block was included to account for possible effects of position of 9 ponds within 3 rows. This analysis proved that the block (i.e., rows) only explained a very small amount of total variance. Hence, we excluded this factor for further analyses.

df, degrees of freedom; F, variance ratio; sig, significance levels of error probability ( $p < 0.001 = ***$ ,  $p < 0.01 = **$ ,  $p < 0.05 = *$ ,  $p < 0.1 = .$ ,  $p > 0.1 = ns$ ); vc (%), relative contribution of individual factors and their interactions to total variance.



**Fig. 3.A1** Two-way-interaction boxplots of total biomass (g) at the end of the flooding experiment: 12 plant species (six species with a preference for either wet or dry microhabitats: wet & dry, respectively) under a flooding duration of 2 and 4 weeks (2w & 4w) and in flooding depth groups of no flooding (i.e., control), partial flooding, and complete flooding (noFI, paFI, coFI). Flooding depth  $\times$  flooding duration interaction (**a**); microhabitat preference  $\times$  flooding duration interaction (**b**); flooding depth  $\times$  microhabitat preference interaction (**c**). Boxes represent the 25th and 75th percentiles and the median value (line); whiskers indicate 1.5 times the interquartile range (or the largest/smallest value in the data if it is lower than 1.5 IQR); points represent outlying data beyond the whiskers.



**Fig. 3.A2** Boxplots of total plant height (mm, **a**) and total biomass (g, **b**) at the end of the flooding experiment: 12 plant species (six species with a preference for either wet or dry microhabitats: wet & dry, respectively) under a flooding duration of 2 and 4 weeks (2w & 4w) and in flooding depth groups of no flooding (i.e., control), partial flooding, and complete flooding (noFI, paFI, coFI). Boxes represent the 25th and 75th percentiles and the median value (line); whiskers indicate 1.5 times the interquartile range (or the largest/smallest value in the data if it is lower than 1.5 IQR); points represent outlying data beyond the whiskers.

## CHAPTER 4

### Modeling of rare flood meadow species distribution by a combined habitat-surface water-groundwater model

Johannes P. Gattringer\*, Nadine Maier\*, Lutz Breuer, Annette Otte, Tobias W. Donath, Philipp Kraft & Sarah Harvolk-Schöning

Submitted manuscript (Ecohydrology)

#### **Abstract**

Floodplains are highly complex and dynamic systems in terms of their hydrology. Thus, they comprise a wide habitat heterogeneity and therefore harbor highly-specialized species. For future projections of habitat and species diversity, process-based models simulating ecohydrological conditions and resulting habitat and species distributions are needed. We present a new modeling framework that includes a physically-based, surface water-groundwater model coupled with a habitat model. Using the model framework, we simulate the occurrence of 23 flood meadow plant species in a Rhine River floodplain. To benchmark the data, results are compared to a conventional approach with simple spatial hydrological information. Our results show that models with predictors obtained from the surface water-groundwater model are significantly more accurate for rare and endangered species, as well as for typical flood meadow species. Therefore, we recommend including more specific hydrological information in habitat models of species in complex floodplain ecosystems.

\* These authors contributed equally to the work

## Introduction

River floodplains comprise a large species diversity, and at the same time, they belong to the most endangered ecosystems worldwide (Ward et al. 1999; Tockner and Stanford 2002; Funk et al. 2013). In regards to their hydrology, they are highly dynamic and complex, because many different components, including surface water, groundwater, and precipitation, are interacting on high temporal and spatial resolution. The driving factor of eco-hydrological functions in floodplains is the connectivity and interaction of shallow groundwater with the surface water due to inundations (Hayashi and Rosenberry 2002; Krause et al. 2007).

In river-fed floodplains, the main driving factor of the water table is the river stage (Acreman and Holden 2013). The response time of the water table to changes in the river stage can be very rapid on a wide spatial extent (Jung et al. 2004). The antecedent soil moisture condition alters the water storage capacity of the soil and thus drives the flood extent, flood duration, and inundation height of water in the floodplain. The actual soil water conditions are not only affected by flood events, but also by previous weather conditions and the ability of the wetland to lose water through soil drainage, evaporation, and transpiration (Acreman and Holden 2013). This complexity in hydrological fluxes and stages is reflected in floodplain's habitat and species diversity.

Species composition in floodplains is influenced by the tolerance of and assimilation to inter-annual-variation of flooding and droughts, the duration and depth of flooding (David 1996; Mathar et al. 2015), as well as the groundwater regimes (Newbold 1997) not only within one year but also during the previous years. Flood meadows are amongst the most threatened plant communities in Central Europe (Joyce and Wade 1998; Finck et al. 2017). Numerous flood meadow species, also called river corridor plants, grow on such flood meadows. These species have adapted to the specific disturbance regimes of floodplains, but they are often rare and/or endangered (Burkart 2001).

Flood meadows are often protected, e.g., by the EU Habitats Directive in Europe, not only because of their diversity and threat of extinction, but also the additional ecosystem services they provide, including flood control. Numerous restoration measures have been implemented to help maintain the diversity of species-rich meadows. These measures primarily focus on the reestablishment of rare species (Donath et al. 2007; Engst et al. 2016). However, the complex hydrological conditions of the target areas (Malanson 1993) often pose a challenge to such restoration projects.

Plant distribution is strongly related to hydrologic conditions that should be considered during restoration, e.g., flood sensitive species occupy elevated microsites, whereas flood tolerant species occur in depressions (Vervuren et al. 2003; Jung et al. 2008; Ludewig et al. 2014). Thus, hydrologic conditions should be incorporated in the planning of flood meadow restoration projects (Gattringer et al. 2017).

Planning, decision-making, and projections for the future require models. Such models need to simulate hydrological processes, and based on this information, define potential habitat characteristics and species abundances. The requirements are high for a hydrological model to simulate the complex hydrodynamic interactions of a floodplain as outlined above. These models need to be capable of simulating water fluxes of and between different landscape components (surface water, groundwater, river water, soil storage, vegetation, and atmosphere) on a high temporal and spatial resolution (Lewin and Hughes 1980). Recently, Maier et al. (2017) presented a parsimonious floodplain model that includes these mechanisms. They used the Catchment Modeling Framework (Kraft et al. 2011) to set up a tailor-made, fully-distributed surface water-groundwater interaction model for the simulation of the height and duration of inundations as well as the flooding frequency, and they applied it to a nature reserve in the Rhine Valley, Germany.

Habitat models have proven to be an ideal tool for enhancing conservation decisions, especially when modelers and conservationists are working closely together, and thus modeling and decision processes are tightly interwoven (Guisan et al. 2013). However, in the past, it was considered a challenge to model the distribution of rare and endangered species (Elith\* et al. 2006; Guisan et al. 2006); rare species datasets are mostly characterized by low occurrences, resulting in potentially over-fitted models when multiple predictors are included (necessary for describing the species' niches) (Lomba et al. 2010). A promising step forward to overcome this obstacle was made by considering model ensembles of small models (ESM) to improve the reliability of habitat models (Breiner et al. 2015; Breiner et al. 2018). Few studies have tested this novel approach, but not for rare flood meadow species (Di Febbraro et al. 2017; Breiner et al. 2018).

So far, only a few studies have used hydrological information to simulate the distribution of riparian vegetation or the occurrence of plant species in these regions. Mosner et al. (2011) employed average water level und water level fluctuation to model the distribution of *Salix* species on 400 km<sup>2</sup> along the Elbe River, and Leyer (2005) utilized a similar approach to simulate the abundance of 30 common grassland species in the Elbe River floodplain. Mosner et al. (2015) computed habitat models by

relating up to five hydrological variables with occurrence records of several floodplain plants along the Upper Rhine River. However, these studies only included static, interpolated hydrological information, such as average groundwater level or its standard deviation. Nevertheless, this does not reflect the actual dynamic hydrological conditions for the plants with varying length and height of inundation.

This study aims to overcome the static approach implemented in most habitat models. Instead, we propose an integrated model approach with biotic and dynamic abiotic processes. With this method, we are able to project species occurrences and habitat suitability in the light of decision-making, management, or global change studies. This study is based on almost 20 years of practical experience in flood meadow restoration, modeling of species distribution, and process-based hydrological model development. We hypothesize that

1. dynamic hydrological predictors improve the credibility of habitat models for floodplains, and
2. detailed hydrological predictors are necessary to accurately model species occurrence, particularly that of rare and endangered species.

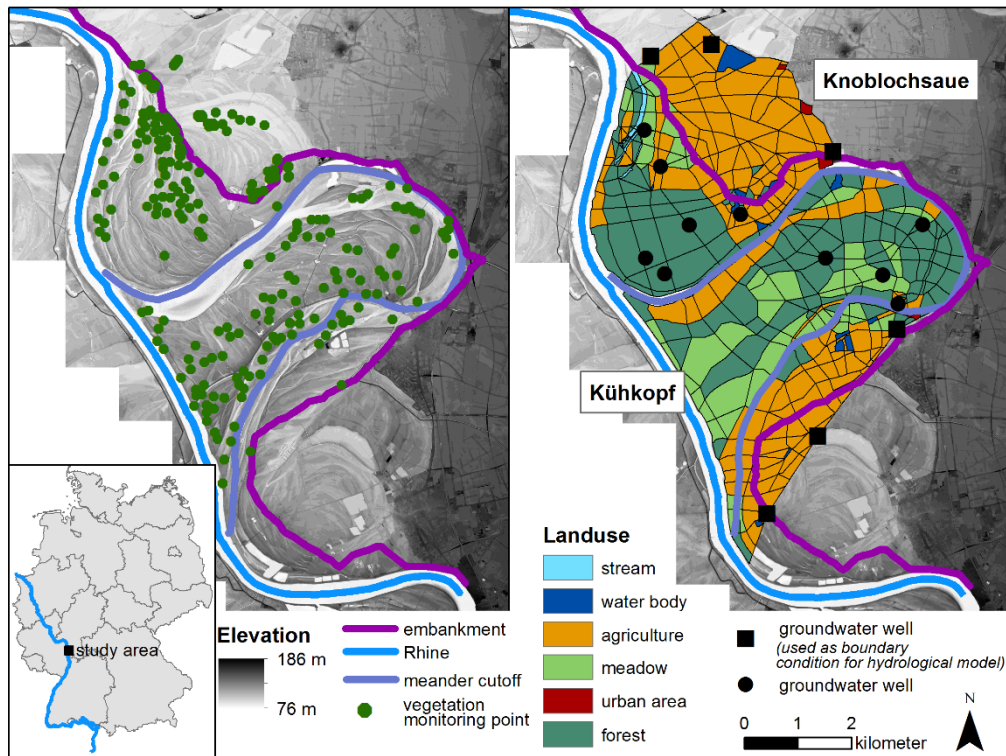
## Materials and methods

### Study area and database

The study area (34.5 km<sup>2</sup>) is located in a Holocene floodplain in the Upper River Rhine approximately 30 km southwest of Frankfurt, Germany (N 49° 49', E 8° 26'). The nature reserve Kühkopf-Knoblochsaue is the largest of its kind in the federal state of Hesse and is declared as a Special Area of Conservation (Council Directive 92/43/EEC) because of its particular importance for rare and endangered flora and fauna. The meander cutoff of the Rhine forms a loop around the Kühkopf island (19.5 km<sup>2</sup>), with a length of about 16 km (Fig. 4.1). Embankments for river regulation were installed in the 19<sup>th</sup> and 20<sup>th</sup> centuries. They divide the area into functional (8.5 km<sup>2</sup>, west of the embankment) and fossil (6.4 km<sup>2</sup>, east of the embankment) floodplain. The two parts vary in their river hydrological connectivity and characteristics, as well as soil types (Böger 1991).

The mean daily temperature is about 10 °C, and the mean relative humidity is 78% (2000–2015). The average annual precipitation is 700 mm (2000–2015). 2006 was a wet year with 925 mm, and 2015 a dry year with only 235 mm precipitation.





**Fig. 4.1** Geographic location of the study area in Germany (lower left corner), digital elevation (Hessian Administration for Soil Management and Geographical Information, HVBG, Wiesbaden, Germany) of the study area with the location of vegetation observations (middle) and setup of the surface water-groundwater model (catchment modeling framework, CMF) with its irregular grid and land use, containing the locations of the groundwater wells (right).

The study area is dominated by a strong seasonal change between floods and droughts. Flooding occurs mainly from February to June and rarely in summer (Böger 1991; Hölzel and Otte 2004). The fine-grained calcareous alluvial soils have high clay contents. Soils desiccate rapidly after the drawdown of floods or high groundwater levels and available soil water content decreases (Burmeier et al. 2010). Flood duration and height vary considerably between the years as well as seasonally. The highest water levels between 2002 and 2013 were reached in April 2003 (87.1 m a.s.l) and March 2003 (86.62 m a.s.l, gauging station Nierstein-Oppenheim, 3 km downstream). All years during the study period had a flood event in the winter.

### *Meteorology*

The meteorological data are provided by the Deutscher Wetterdienst (DWD) in daily time steps and include minimum and maximum temperature, mean relative humidity, mean wind speed, and precipitation. The meteorological data are used to force the

surface water-groundwater model. Five meteorological predictors for the habitat model are directly generated from the daily precipitation records.

### *Hydrology*

Weekly measurements of 15 groundwater wells are available for the study area (Hessian Agency for Nature Conservation, Environment and Geology (HLNUG)). Six groundwater wells are installed in the fossil floodplain and there are nine wells in the functional floodplain (Fig. 4.1). The groundwater level time series of the groundwater wells in the floodplain correlate, with a short time lag, with the water level time series of the Rhine. The flood signal smooths out with increasing distance from the river. In case daily water levels are needed, linear interpolation is used.

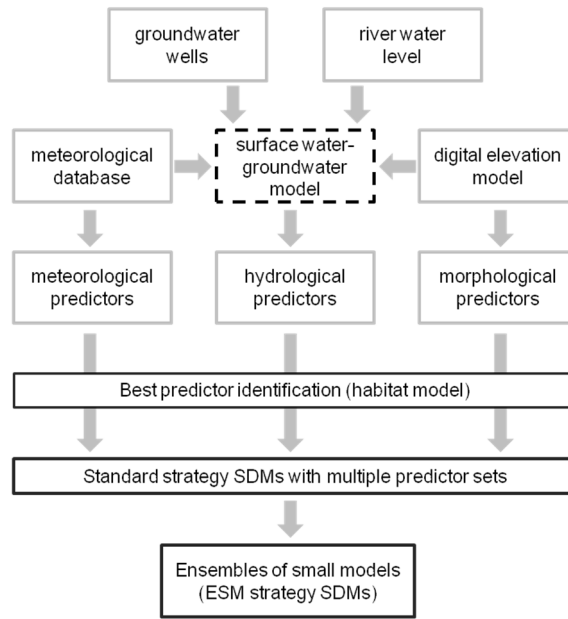
The water level of the Rhine River is obtained from the FLYS software (Flusshydrologischer Webdienst, German Federal Institute of Hydrology, BfG, Koblenz, Germany) for every 100 m along the Rhine River (values for river-kilometers 468 to 480 were considered).

### *Plant species*

The 23 plant species used for modeling in this study (Annex 4 Table 4.A1) were target species in numerous restoration projects focusing on the reestablishment of species-rich flood meadows along the northern Upper Rhine (Donath et al. 2007). In total, 226 vegetation plots with information on presence and absence of target species served as basis for the habitat modeling (for further information on vegetation data, see Annex 4 Table 4.A1).

## **Integrated model setup**

In the following section, the different steps implemented in this study are explained in detail. Figure 4.2 represents the main steps in the modeling process. The surface water-groundwater model depicts the main component for the hydrological representation of the floodplain and the basis for the hydrological predictors of the habitat model. The model is fed by data from the meteorological database and the digital elevation model, as well as other hydrological data (groundwater levels and river water stages). Alongside the hydrological predictors, meteorological and morphological predictors were also derived. After the identification of the best and most powerful predictors, the best 100 predictor sets were used for the calculation of ensembles of small models (ESM strategy).



**Fig. 4.2** Representation of the main steps of the integrated model setup. ESM=Ensembles of Small Models, SDM=Species Distribution Model. The grey boxes depict input data for the following steps. The black boxes indicate modeling steps. The surface water-groundwater model is described in the Methodology section (dashed black box). The solid black boxes depict the main results and are described in the results section.

### *Surface water-groundwater model*

In order to simulate the high-resolution input data (temporal and spatial) of groundwater levels and inundation events required for the habitat model, we developed a spatially explicit, fully-distributed dynamic surface water-groundwater model. Full details about the hydrological model setup are described in Maier et al. (2017). In short, the model is built with the Catchment Modeling Framework (CMF) (Kraft et al. 2011) and includes the interaction of surface water and groundwater flow. As input data, the model requires daily stream water levels (in our case study, data from the Rhine River) and weekly groundwater levels at the upslope, daily minimum and maximum temperature and relative humidity for the estimation of potential evapotranspiration, and daily precipitation. The floodplain is split into the two regions Kühkopf and Knoblochsau (Fig. 4.1). These are further subdivided into polygons ( $n=657$ ) of different sizes ( $114-480,000 \text{ m}^2$ ), based on similar elevation and land use. For simplicity, the polygons are not further discretized vertically. For each region, the water level of the Rhine and groundwater levels of three monitoring wells are used as input data (Dirichlet boundary conditions). Initial conditions, i.e., the water level of each polygon at the first day of simulation, are calculated using external drift

kriging (Goovaerts 1997). To evaluate the surface water-groundwater model, we use observation data from four to six groundwater monitoring wells in each region. We ran 5,000 simulations following a Latin Hypercube sampling procedure to derive behavioral model runs. We receive a mean root-mean-square error of 0.25 m (Knoblochsaue) and 0.39 m (Kühkopf) for the different groundwater wells for the calibration period of 2.5 years (7.1.2002–30.6.2004), and 0.23 m (Knoblochsaue) and 0.36 m (Kühkopf) for the validation period of 9.5 years (1.7.2004–31.12.2013). As model output, we obtain the water level for the center of each polygon. We use the mean of all behavioral model runs to further estimate the hydrological predictors for the habitat model. The daily water level of each vegetation plot is estimated by inverse distance weighting. Hydrological predictors for the habitat model were calculated from the obtained daily time series of each vegetation plot.

#### *Habitat model*

Due to the large number of potential hydrological predictors, we follow a three-tiered approach in our modeling cascade to reduce the high computational effort of the final habitat model. As the first step, we identify predictor variables with high explanatory power. Second, we identify the best predictor sets using standard strategy SDMs (species distribution models). Third, we compute ensembles of small bivariate SDMs using the best predictor sets from the second step to overcome possible limitations of standard strategy SDMs due to low presence levels of the modeled species.

##### *1) Best predictor identification*

To identify relevant predictors for species distribution, we established single predictor SDMs for seven target species (i.e., *Arabis nemorensis*, *Centaurea jacea*, *Inula silicina*, *Leucanthemum vulgare*, *Ranunculus acris*, *Sanguisorba officinalis*, and *Veronica maritima*) with acceptable occurrence levels within the study area. These seven target species are representative for the total list of the 23 target species (Annex 4 Table 4.A1). We selected species with low ( $< 26$ ) or high ( $> 50$ ) occurrences in the database in combination with species of high relatedness to flood meadows (Burkart=1) or ubiquitous distribution ranges (Burkart=0). We computed generalized linear models (GLMs using the BIOMOD framework (Thuiller et al. 2009)) by relating predictors separately with presence-absence of the seven target species. To evaluate the models, we calculated Nagelkerke's  $R^2$  value (Nagelkerke 1991) for the single predictor SDMs to identify predictors with a large explanatory power. Based on these results, we rejected predictors with little to no explanatory power (i.e., not among the best 50% for most species) or predictors with almost identical information.

The environmental variables used for the species distribution modeling are time invariant (Mieszkowska et al. 2013), whereas the water table and the meteorological conditions vary over time. The meteorological conditions are assumed to be the same over the entire study area. In contrast, the groundwater water table is not static over time or space. To overcome this issue, we transformed the time series into hydrological predictors.

For each vegetation plot, we generated 81 hydrological predictors (Annex 4 Table 4.A2). These predictors are based on various experimental studies (e.g., Van Eck et al. 2004; Gattringer et al. 2017, Gattringer et al. 2018) or observational studies (e.g., Leyer 2005; Mosner et al. 2015). We derived the hydrological predictors either for the entire year or only for the vegetation period, and we considered up to six years before the monitoring year, thus resulting in  $n=14$  different variations. Beyond that, we identified five meteorological and nine morphological predictors. We used all predictors and time periods to perform single predictor SDMs. Consequently, we computed 1,213 single predictor SDMs per species ((81 hydrological predictors + 5 meteorological predictors)  $\times$  14 time periods + 9 morphological predictors).

### *2) Standard strategy SDMs with multiple predictor sets*

In the next step, we computed standard strategy SDMs with multiple predictor sets from the selected best predictor variables from the single predictor SDMs. Therefore, we calculated GLMs using the BIOMOD framework (Thuiller et al. 2009) for all 23 species. We used all possible combinations of predictors (i.e., predictor sets) that were not correlated according to the rule of thumb as set by Dormann et al. (2013), i.e., correlation coefficients of predictors from a set of 10,000 random points should not exceed 0.7. We calculated Nagelkerke's  $R^2$  value (Nagelkerke 1991) based on a repeated (3 times) split-sampling approach, in which models were calibrated with 80% of the data and evaluated over the remaining 20%. We chose the best 100 predictor sets of each species for the subsequent modeling based on the mean  $R^2$  over the three data splits.

### *3) Ensembles of small models (ESM strategy SDMs)*

When computing models for rare and endangered species, which are fitted with a high number of predictors, model overfitting may occur. This overfitting can result in decreased generalizability of the models (Vaughan and Ormerod 2005). To overcome these limitations of standard strategy SDMs of rare species, we computed ensembles of small bivariate SDMs (ESM strategy SDMs) as described by Breiner et al. (2015), which means ESM strategy SDMs are based on a two-step approach. First, bivariate

models of all possible twofold combinations of predictors are calibrated and evaluated separately (i.e., by means of the **area under the receiver operating characteristic curve**; AUC (Hanley and McNeil 1982)). Second, ensemble models are computed and evaluated (by means of AUC and true skills statistic (TSS)) as a weighted average by means of Somers' D with a threshold of 0, where Somers' D = 2 x AUC - 1 of the bivariate models. This approach avoids overfitting without reducing the number of predictor variables and thus without loss of explanatory power (Breiner et al. 2015). We used predictor sets with up to ten predictors and computed ESM strategy SDMs for the target species. We utilized the R-package *ecospat* (Broennimann et al. 2016) and a 80:20 cross validation procedure (ten data splits) to calculate the AUC and the TSS (Allouche et al. 2006).

### **Model evaluation**

As we hypothesized that the integrated surface water-groundwater-species distribution model would be superior in simulating species distribution of flood meadows, we rigorously tested our approach. Therefore, we compared model results calculated with hydrological predictors from the surface water-groundwater model with results of a habitat model using similar hydrological predictors, which have been derived from other data sources (i.e., different predictor calculation databases). In one case, we derived the hydrological predictors from daily water levels of the Rhine River and extrapolated to the floodplain (riv, Table 4.1). In the second case, we used the weekly measured groundwater data, and interpolated to daily time steps and extrapolated to the floodplain (gww, Table 4.1). This benchmark approach followed the same procedure as for the surface water-groundwater model. The meteorological and morphological predictors remained the same for both applications. Additionally, to account for the explanatory power of the hydrological variables alone, we also ran the habitat model without any hydrological predictors (nhy, Table 4.1).

To test for differences in modeling results between the predictor calculation databases, we calculated linear mixed-effects models according to Zuur et al. (2009) (function *lme* in the R-package *nlme*) (Pinheiro et al. 2017). Here, we chose a subset of the seven best predictor sets for every species and every predictor calculation database, because we wanted to identify the best predictor sets – and in the next step, the best explaining predictors. We used – as proxies for quality of habitat models – Fisher-Z-transformed AUC and Fisher-Z-transformed TSS as response variables, the hydrological calculation method as fixed effect, and the factor species as a random effect in the mixed models. We subsequently computed post hoc Tukey contrasts for pairwise comparisons (function *glht* in the R-package *multcomp*) (Hothorn et al. 2008). To

**Table 4.1** Definition of the four predictor calculation databases used for the evaluation of the habitat model. The superscript indicates for which predictor the input data are relevant.

	Hydrological predictor derived from ...	Included predictors	Used input data
<b>sgm</b>	surface water-	(1) hydrological	water levels of the Rhine River <sup>(1)</sup> ,
	groundwater model	(2) meteorological	groundwater levels <sup>(1)</sup> , DEM <sup>(1),(3)</sup> ,
		(3) morphological	meteorological data <sup>(1),(2)</sup>
<b>gww</b>	groundwater wells (observation data, n=16, Fig. 4.1)	(1) hydrological	groundwater levels <sup>(1)</sup> , DEM <sup>(1),(3)</sup> ,
		(2) meteorological	meteorological data <sup>(2)</sup>
		(3) morphological	
<b>riv</b>	simulated water levels of the Rhine River (FLYS)	(1) hydrological	water levels of the Rhine River <sup>(1)</sup> ,
		(2) meteorological	DEM <sup>(1),(3)</sup> , meteorological data <sup>(2)</sup>
		(3) morphological	
<b>nhy</b>	(no hydrological data)	(2) meteorological (3) morphological	meteorological data <sup>(2)</sup> , DEM <sup>(3)</sup>

compare the influence of the predictor calculation database on model success for individual species, we then calculated ANOVAs for every species separately and subsequently computed post hoc Tukey HSD tests for pairwise comparisons.

Additionally, we accounted for possible impacts of rarity and Red List status of plants on model quality. To do this, we tested whether or not including the factors (i) Red List status in Hesse (Hemm et al. 2008), and (ii) the classification as a flood meadow species according to Burkart (2001) (Annex 4 Table 4.A1) considered as fixed factors in linear mixed-effects models lead to differences in AUC or TSS values.

Finally, yet importantly, we evaluated the relative frequency of hydrological predictors in the best seven predictor sets per species to account for their relevance. The habitat modeling, analysis, and data visualization were carried out in R 3.4.2 (R Core Team 2017) and ggplot2 2.2.1 (Wickham 2009).

## Results

### Best predictor identification

Based on the modeling results with the 95 a priori defined predictors (81 hydrological, 5 meteorological, and 9 morphological predictors, Annex 4 Table 4.A2), we selected 19 significant and differentiating predictors for multi-predictor SDMs. The

hydrological predictors can be grouped by their indication of drought, wetness, or inundation. A detailed description of the selected predictors is given in Table 4.2. The largest explanatory value for the individual predictors was obtained if the vegetation period of the previous six years (before the vegetation survey date) was considered. As a result, we used only this period for the 16 time-dependent predictors (PH01–PH15 and PM16).

From the 19 predictors (Table 4.2), we defined predictor combinations following the rule of thumb as defined by Dormann et al. (2013). As predictor correlations are likely different for each of the three predictor calculation databases (Table 4.1), we defined individual predictor sets for each predictor calculation database. The maximum number of predictors for a set was 10, 9, and 8 predictors for the sgm, gww, and riv predictor calculation databases, respectively. In total, 25,252 (sgm), 9,052 (gww), and 7,540 (riv) predictor sets were possible.

### **Evaluation of habitat model**

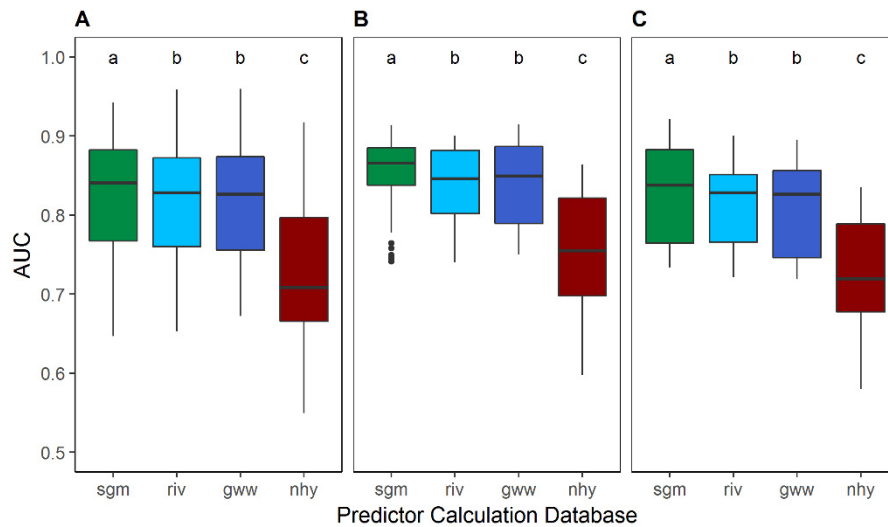
Overall, the mean AUC was highest for the sgm predictor calculation database ( $0.83 \pm \text{SE } 0.006$ ), followed by gww ( $0.82 \pm \text{SE } 0.006$ ), riv ( $0.81 \pm \text{SE } 0.006$ ), and nhy ( $0.72 \pm \text{SE } 0.008$ ) (Fig. 4.3A). Evaluations of habitat models based on AUC were highly correlated with evaluations based on TSS (Pearson correlation coefficient = 0.94;  $p < 0.001$ ); therefore, we present only AUC results. Linear mixed-effects models showed that models with hydrological predictors result in better evaluation scores than models without hydrological predictors (nhy,  $p < 0.001$ , Fig. 4.3A). Furthermore, AUC was higher for the sgm predictor calculation database in comparison to the riv and gww predictor calculation databases ( $p < 0.05$ ). Habitat model performance also differed significantly for endangered and vulnerable Red List species (Fig. 4.3B), as well as when only flood meadow species according to Burkart were assessed (Fig. 4.3C).



**Table 4.2** Selected predictors used as input data for the multi-predictor species distribution models.

Predictor	Description	Indication
PH01	Standard deviation of the groundwater level (m)	
PH02	Absolute range of the groundwater level (m)	
PH03, PH04, PH05	Longest period during which the groundwater level was less than 1 m / 1.5 m / 2.5 m below ground (days)	Drought
PH06, PH07	Longest period during which the groundwater level was more than 2.5 m / 0.5 m below ground (days)	Wetness
PH08, PH09	Sum of days on which the groundwater level is more than 2.5 m / 0.7 m below ground (days)	Drought (Wetness)
PH10	Sum of days on which the inundation height was a minimum 50 cm (days)	Inundation
PH11	Longest period during which the inundation height was a minimum 50 cm (days)	Inundation
PH12, PH13, PH14	Sum of days on which the groundwater level was less than 50 cm below ground and the daily precipitation was less than 1 mm during the first 60 / 80 / 100 days of the vegetation period (days)	Drought
PH15	Sum of days on which the groundwater level was less than 50 cm below ground and the daily precipitation was above 1 mm during the first 100 days of the vegetation period (days)	Wetness
PM16	Longest period of wet days (daily precipitation > 1 mm) (days)	
PN17*	Height above sea level, derived from the digital elevation model (m)	
PN18*	Distance to the Rhine or the meander cutoff (m)	
PN19*	Distance to any water surface (distance to Rhine, the meander cutoff or lake) (m)	

PH=hydrological predictors, PM=meteorological predictors, PN=morphological predictors, \*=time independent predictors (i.e., same value for all years and periods)

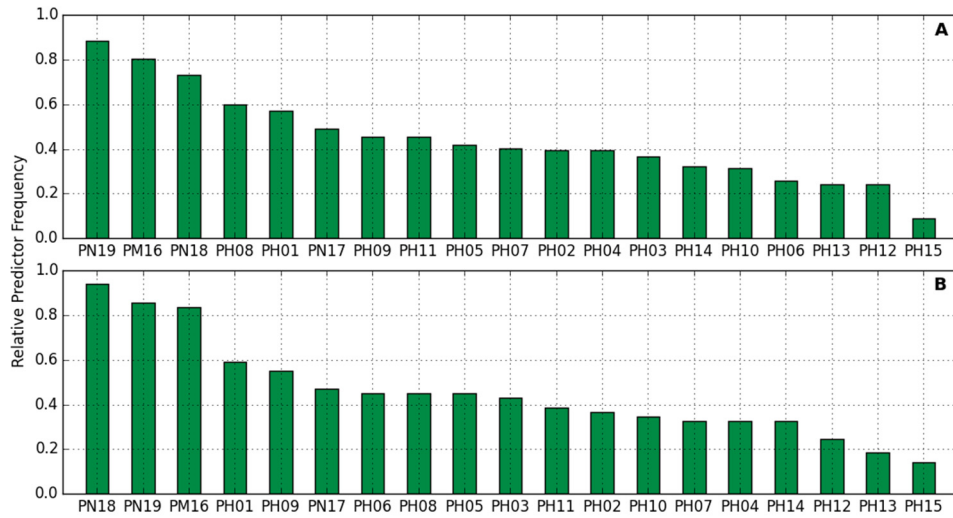


**Fig. 4.3** Simulated area under the receiver operating characteristic curve (AUC) for flood meadow species without using hydrological predictors (nhy), using hydrological predictors derived from the surface-groundwater-model (sgm), measured groundwater data (gww), and simulated water level of the Rhine River (riv). (A) Results for all 23 species. (B) Results for endangered and vulnerable species listed on the Red List in Hesse (Hemm et al. 2008). (C) Results for flood meadow species according to Burkart (2001). Letters denote significant differences across predictor calculation databases ( $p < 0.05$ ).

For single species, habitat models with predictors from the sgm database outperform other predictor calculation databases in almost half of the modeled species (10 of 23), followed by models with predictors from the gww (9 of 23) and riv databases (4 of 23) (Annex 4 Fig. 4.A1). ANOVA revealed that 2 out of the 10 species showed significantly better habitat model quality for the sgm input data. In general, models with hydrological predictors (sgm, riv, gww) significantly outperformed the models without hydrological predictors (nhy). Including hydrological predictors, and in particular, those resulting from the surface water-groundwater model, lead to better habitat model results. Therefore, from here on, we present only results of the habitat model based on the hydrological predictors obtained from the surface water-groundwater model.

### Significance of individual predictor variables

A set of 19 predictors for the simulation of species habitats may seem large; however, given that we simulate vulnerable, endangered, and flood meadow species, specific predictors might be needed to project the occurrence for specific individual species. We therefore analyzed the occurrence of predictors for each of the 23 species. For both species groups (flood meadow species, and vulnerable and endangered Red List



**Fig. 4.4:** Relative predictor frequency for all model runs separated for the (A) flood meadow species according to Burkart and (B) species on the Red List (vulnerable and endangered).

species), five predictors are used in over 50% of the model runs (Fig. 4.4), of which four are the same (PN19, PN18, PH16, PH01). For the flood meadow species, the predictor PH08 was used, and for the vulnerable and endangered Red List species, the predictor PH09 is used more frequently. Both predictors are based on the same measurement, i.e., the sum of days on which the groundwater level exceeds a certain level (PH08: 2.5 m below ground; PH09: 0.7 m below ground). The least common predictors for both species groups are predictors PH12, PH13, and PH15 (< 25%; Fig. 4.4). Nevertheless, predictors PH12 and PH13 are relevant in models of 5 Red List and 7 flood meadow species, and even the least common predictor PH15 contributes to about 10% of the habitat models (in 1 flood meadow and 3 Red List species).

## Discussion

### Relevance of hydrological predictors for flood meadow habitat simulations

The aim of our study was to assess possible options to include hydrological information in habitat modeling of flood meadow species. The significance of water level fluctuations and water level variability for ecological modeling of wetlands has been emphasized by several studies (e.g., Leyer 2005; Kopeć et al. 2013). We included hydrological predictors from a dynamic surface water-groundwater model in a habitat

model, and found a significant improvement of the model quality compared to habitat models derived only from morphological data (Fig. 4.3).

Only few studies have linked detailed hydrological variables to habitat models (e.g., Mosner et al. 2011; Mosner et al. 2015). Mosner et al. (2011) derived their hydrological predictors from a combination of river water level and groundwater data from the adjacent river (similar to our gww database), while variables in Mosner et al. (2015) were derived from a model of the adjacent river (similar to our riv dataset). Our results showed a significant model improvement when utilizing hydrological predictors from the surface water-groundwater model (sgm database) over the two other possibilities. We conclude that for rare species the complexity of habitat requirements can be better described with predictors from a detailed and spatially explicit hydrological model than with interpolated, measured hydrological variables.

### **Specialized species need specific predictors**

As for most modeling approaches, it seems desirable to reduce the complexity of model input data to help simplify models. Mosner et al. (2011) and (2015) modeled species occurrence with only two predictors, i.e., water level and water level fluctuations of the adjacent river. Our results suggest that more (i.e., from 6 to 10) specific predictors are needed to simulate habitats and occurrences for the rare and endangered species. In comparison to the study by Mosner et al. (2011), we included more specified predictors (e.g., longest period of days with a specific water level or specific inundation height), and we showed that those predictors are used relatively often. For flood meadow species and vulnerable and endangered Red List species, two morphological, one meteorological, and two hydrological predictors (standard deviation and sum of days with low ground water level) are used in over 50% of all final habitat model runs (Fig. 4.4). Only three of the 19 predictors we identified are used less frequently than in one-fourth of all model runs. Nevertheless, they are relevant to predict the occurrence of all flood meadow and Red List species. Those three predictors refer to periods with dry soil in the first days of the growing period. Reversely, this means wet soil conditions are relevant for flood meadow species and especially for vulnerable and endangered Red List species. This is in line with Boswell et al. (2007), who designated the duration of saturation at the surface and at the saturation in the root zone, as well as the distribution of open water, as essential hydrological variables for modeling groundwater-dominated wetland habitats.

Our most frequently used hydrological predictors included values indicating dry conditions, wet conditions, or inundation length. This provides evidence that the

habitat requirements of flood meadow species are complex. They are not only able to cope with flooding, but also with drought periods (Burkart 2001), and thus one requires multiple variables in order to properly represent this complex environment. Other than the hydrological predictors, two morphological predictors (i.e., distance to the river or water surfaces) are frequently considered in our habitat models. In literature, these predictors are seen as proxies for several factors (e.g., soil texture) (He and Walling 1998; Leyer 2005), which affect species distribution and are linked to the distance to the river. Thus, those morphological predictors are generally useful for floodplain species' modeling in case there is an absence of other data (Mosner et al. 2015). Furthermore, in our study, the distance to water seems to reflect the land-use legacies: The target species mostly occur on "original" sites (i.e., in close proximity to the river) where the ancient habitat conditions were sufficient for the plants to colonize, and they could persevere on these sites to the present, despite the strong impacts of land use in the past centuries (Böger 1991).

This study revealed that more specified hydrological predictors should be considered when modeling species' distribution, and that it is important from which data sources these hydrological predictors are generated. Chui et al. (2011) stated the importance of models for generating hydrological predictors, considering surface hydrology and surface water-groundwater interactions. Boswell et al. (2007) also believed in the great implication of hydrological modeling for planning and prioritization of wetland restoration. However, despite their suggestions, we are not aware of any integrated model approach that has been developed and successfully applied to simulate not only flood meadow species in general, but also the occurrence of rare and endangered species.

## **Conclusion and further applications**

We conclude that habitat models achieve better results when hydrological predictors of a detailed surface water-groundwater model are included. Averaged over all species, the results are marginally, yet still significantly, better when compared to habitat models based on readily available observation data alone (groundwater level, river water level). However, a clear advantage of utilizing complex hydrological models for predictor generation is obvious for rare specialist species with complex habitat requirements. Particularly for such species, habitat models should include detailed hydrological predictors with high temporal and spatial resolution. We recognize two prominent fields, in which spatially explicit habitat models, like those developed in this study, are needed: (1) conservation planning and (2) global change studies.

In today's conservation planning, the decisions about whether a specific site is suitable and promising for restoration are often based on soft data and subjective appreciation. This method often neglects elevation or small-scale spatial variation in soil conditions. We question whether the current method of spending large amounts of money for such restoration without considering site-specific characteristics is the way forward. Applications of complex habitat models possess the power to improve conservation outcomes (Guisan et al. 2013), by identifying suitable habitats prior to management activities.

To evaluate the global change impact, such as land management and/or climate change, process-based hydrological models are a good choice. Our habitat model is capable of simulating changes in vegetation cover (selection of species, changes in land management), morphological characteristics (floodplain reconstruction, construction of embankments, river regulation) and climate (precipitation amounts and seasonal patterns, temperature affecting evapotranspiration). For example, it is possible to run the model with different land-use change scenarios (Maier et al. 2018). The resulting water levels can be integrated in the habitat models, and predictions can be made for species occurrence and recommendations for wetland restoration under the hypothetical and predicted land use changes. Furthermore, the hydrological model can be forced by climate change projections. Thus, hydrological predictors over several years in the near and distant future can be derived. The species distribution model can then be used to make predictions for future species occurrence (Elith and Leathwick 2009) and particularly for rare and endangered species.

## Acknowledgements

This research was funded by the Deutsche Bundesstiftung Umwelt (DBU; Project-No. 31612/01; [www.dbu.de](http://www.dbu.de)). The funder had no role in the study design, data collection and analysis, decision to publish, or preparation of the manuscript. We thank all contributors of vegetation data for their willingness to share datasets, i.e., the KLIWAS project group and the City of Riedstadt. The climate data are available from the Germany's national meteorological service (Deutscher Wetterdienst (DWD), <http://www.dwd.de/cdc>; <ftp://ftp-cdc.dwd.de/pub/CDC>). Daily water levels from the gauging station Nierstein are available from the Federal Waterways and Shipping Authority (Wasser und Schifffahrtsverwaltung des Bundes (WSV)) and provided by the Federal Institute of Hydrology (Bundesanstalt für Gewässerkunde (BfG)). Groundwater levels are provided by the Hessian Agency for Nature Conservation,

Environment and Geology (Hessisches Landesamt für Naturschutz, Umwelt und Geologie (HLNUG)). The digital elevation model (DEM) was provided by the Hessian State Office of Land Management and Geological Information (Hessisches Landesamt für Bodenmanagement und Geoinformation (HLBG)).

## References

- Acreman M, Holden J (2013) How Wetlands Affect Floods. *Wetlands* 33:773–786. doi: 10.1007/s13157-013-0473-2
- Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J Appl Ecol* 43:1223–1232. doi: 10.1111/j.1365-2664.2006.01214.x
- Böger K (1991) Grünlandvegetation im Hessischen Ried. Pflanzensoziologische Verhältnisse und Naturschutzkonzeption (Grassland vegetation in the Hessian Ried. Plant sociology and nature conservation concept). Botanische Vereinigung für Naturschutz in Hessen (BVNH), Frankfurt/Main
- Boswell JS, Olyphant GA (2007) Modeling the hydrologic response of groundwater dominated wetlands to transient boundary conditions: Implications for wetland restoration. *J Hydrol* 332:467–476. doi: 10.1016/j.jhydrol.2006.08.004
- Breiner FT, Guisan A, Bergamini A, Nobis MP (2015) Overcoming limitations of modelling rare species by using ensembles of small models. *Methods Ecol Evol* 6:1210–1218. doi: 10.1111/2041-210X.12403
- Breiner FT, Nobis MP, Bergamini A, Guisan A (2018) Optimizing ensembles of small models for predicting the distribution of species with few occurrences. *Methods Ecol Evol* 9:802–808. doi: 10.1111/2041-210X.12957
- Broennimann O, Di Cola V, Guisan A (2016) ecospat: Spatial Ecology Miscellaneous Methods. R package version 2.1.1
- Burkart M (2001) River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. *Glob Ecol Biogeogr* 10:449–468. doi: 10.1046/j.1466-822x.2001.00270.x
- Burmeier S, Eckstein RL, Otte A, Donath TW (2010) Desiccation cracks act as natural seed traps in flood-meadow systems. *Plant Soil* 333:351–364. doi: 10.1007/s11104-010-0350-1
- Chui TFM, Low SY, Liang S-Y (2011) An ecohydrological model for studying groundwater–vegetation interactions in wetlands. *J Hydrol* 409:291–304. doi: 10.1016/j.jhydrol.2011.08.039
- David PG (1996) Changes in plant communities relative to hydrologic conditions in the Florida Everglades. *Wetlands* 16:15–23. doi: 10.1007/BF03160642

- Di Febbraro M, Carotenuto F, Castiglione S, Russo D, Loy A, Maiorano L, Raia P (2017) Does the jack of all trades fare best? Survival and niche width in Late Pleistocene megafauna. *J Biogeogr* 44:2828–2838. doi: 10.1111/jbi.13078
- Donath TW, Bissels S, Hölzel N, Otte A (2007) Large scale application of diaspore transfer with plant material in restoration practice – Impact of seed and microsite limitation. *Biol Conserv* 138:224–234. doi: 10.1016/j.biocon.2007.04.020
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T, McClean C, Osborne PE, Reineking B, Schröder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46. doi: 10.1111/j.1600-0587.2012.07348.x
- Elith\* J, Graham\* CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberón J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29:129–151. doi: 10.1111/j.2006.0906-7590.04596.x
- Elith J, Leathwick JR (2009) Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annu Rev Ecol Evol Syst* 40:677–697. doi: 10.1146/annurev.ecolsys.110308.120159
- Engst K, Baasch A, Erfmeier A, Jandt U, May K, Schmiede R, Bruelheide H (2016) Functional community ecology meets restoration ecology: Assessing the restoration success of alluvial floodplain meadows with functional traits. *J Appl Ecol* 53:751–764. doi: 10.1111/1365-2664.12623
- Finck P, Heinze S, Raths U, Riecken U, Ssymank A (2017) Rote Liste der gefährdeten Biotoptypen Deutschlands. Dritte fortgeschriebene Fassung (Red list of threatened habitat types in Germany. Third updated version). *Naturschutz Biol Vielfalt* 156:1–460
- Funk A, Gschöpf C, Blaschke AP, Weigelhofer G, Reckendorfer W (2013) Ecological niche models for the evaluation of management options in an urban floodplain—conservation vs. restoration purposes. *Environ Sci Policy* 34:79–91. doi: 10.1016/j.envsci.2012.08.011
- Gattringer JP, Donath TW, Eckstein RL, Ludewig K, Otte A, Harvolk-Schöning S (2017) Flooding tolerance of four floodplain meadow species depends on age. *PLoS ONE* 12:e0176869. doi: 10.1371/journal.pone.0176869
- Gattringer JP, Ludewig K, Harvolk-Schöning S, Donath TW, Otte A (2018) Interaction between depth and duration matters: flooding tolerance of 12 floodplain meadow species. *Plant Ecol* 219:973–984. doi: 10.1007/s11258-018-0850-2
- Goovaerts P (1997) *Geostatistics for natural resources evaluation*. Oxford University Press, New York



- Guisan A, Broennimann O, Engler R, Vust M, Yoccoz NG, Lehmann A, Zimmermann NE (2006) Using Niche-Based Models to Improve the Sampling of Rare Species. *Conserv Biol* 20:501–511. doi: 10.1111/j.1523-1739.2006.00354.x
- Guisan A, Tingley R, Baumgartner JB, Naujokaitis-Lewis I, Sutcliffe PR, Tulloch AIT, Regan TJ, Brotons L, McDonald-Madden E, Mantyka-Pringle C, Martin TG, Rhodes JR, Maggini R, Setterfield SA, Elith J, Schwartz MW, Wintle BA, Broennimann O, Austin M, Ferrier S, Kearney MR, Possingham HP, Buckley YM (2013) Predicting species distributions for conservation decisions. *Ecol Lett* 16:1424–1435. doi: 10.1111/ele.12189
- Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology* 143:29–36. doi: 10.1148/radiology.143.1.7063747
- Hayashi M, Rosenberry DO (2002) Effects of Ground Water Exchange on the Hydrology and Ecology of Surface Water. *Ground Water* 40:309–316. doi: 10.1111/j.1745-6584.2002.tb02659.x
- He Q, Walling DE (1998) An investigation of the spatial variability of the grain size composition of floodplain sediments. *Hydrol Process* 12:1079–1094. doi: 10.1002/(SICI)1099-1085(19980615)12:7<1079::AID-HYP642>3.0.CO;2-E
- Hemm K, Frede A, Kubosch R, Mahn D, Nawrath S, Uebeler M, Barth U, Gregor T, Buttler KP, Hand R, Cezanne R, Hodvina S, Huck S (2008) Rote Liste der Farn- und Samenpflanzen Hessens (Red list of fern and seed plants in Hesse), 4th edn. Hessisches Ministerium für Umwelt, ländlichen Raum und Verbraucherschutz (HMULV), Wiesbaden
- Hölzel N, Otte A (2004) Inter-annual variation in the soil seed bank of flood-meadows over two years with different flooding patterns. *Plant Ecol* 174:279–291. doi: 10.1023/B:VEGE.0000049108.04955.e2
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. *Biom J* 50:346–363. doi: 10.1002/bimj.200810425
- Joyce CB, Wade PM (1998) Wet Grasslands: A European Perspective. In: Joyce CB, Wade PM (eds) *European Wet Grasslands: Biodiversity, Management and Restoration*. Wiley, Chichester, UK, pp 1–12
- Jung M, Burt TP, Bates PD (2004) Toward a conceptual model of floodplain water table response. *Water Resour Res* 40:565. doi: 10.1029/2003WR002619
- Jung V, Hoffmann L, Muller S (2008) Ecophysiological responses of nine floodplain meadow species to changing hydrological conditions. *Plant Ecol* 201:589–598. doi: 10.1007/s11258-008-9508-9
- Kopeć D, Michalska-Hejduk D, Krogulec E (2013) The relationship between vegetation and groundwater levels as an indicator of spontaneous wetland restoration. *Ecol Eng* 57:242–251. doi: 10.1016/j.ecoleng.2013.04.028
- Kraft P, Vaché KB, Frede H-G, Breuer L (2011) CMF: A Hydrological Programming Language Extension For Integrated Catchment Models. *Environ Model Softw* 26:828–830. doi: 10.1016/j.envsoft.2010.12.009

- Krause S, Bronstert A, Zehe E (2007) Groundwater–surface water interactions in a North German lowland floodplain – Implications for the river discharge dynamics and riparian water balance. *J Hydrol* 347:404–417. doi: 10.1016/j.jhydrol.2007.09.028
- Lewin J, Hughes D (1980) Welsh floodplain studies. *J Hydrol* 46:35–49. doi: 10.1016/0022-1694(80)90034-7
- Leyer I (2005) Predicting plant species’ responses to river regulation: the role of water level fluctuations. *J Appl Ecol* 42:239–250. doi: 10.1111/j.1365-2664.2005.01009.x
- Lomba A, Pellissier L, Randin C, Vicente J, Moreira F, Honrado J, Guisan A (2010) Overcoming the rare species modelling paradox: A novel hierarchical framework applied to an Iberian endemic plant. *Biol Conserv* 143:2647–2657. doi: 10.1016/j.biocon.2010.07.007
- Ludewig K, Korell L, Löffler F, Scholz M, Mosner E, Jensen K (2014) Vegetation patterns of floodplain meadows along the climatic gradient at the Middle Elbe River. *Flora - Morphol Distrib Funct Ecol Plants* 209:446–455. doi: 10.1016/j.flora.2014.04.006
- Maier N, Breuer L, Chamorro A, Kraft P, Houska T (2018) Multi-Source Uncertainty Analysis in Simulating Floodplain Inundation under Climate Change. *Water* 10:809. doi: 10.3390/w10060809
- Maier N, Breuer L, Kraft P (2017) Prediction and uncertainty analysis of a parsimonious floodplain surface water-groundwater interaction model. *Water Resour Res* 53:7678–7695. doi: 10.1002/2017WR020749
- Malanson GP (1993) *Riparian Landscapes*. Cambridge University Press, Cambridge
- Mathar W, Kleinebecker T, Hölzel N (2015) Environmental variation as a key process of co-existence in flood-meadows. *J Veg Sci* 26:480–491. doi: 10.1111/jvs.12254
- Mieszkowska N, Milligan G, Burrows MT, Freckleton R, Spencer M (2013) Dynamic species distribution models from categorical survey data. *J Anim Ecol* 82:1215–1226. doi: 10.1111/1365-2656.12100
- Mosner E, Schneider S, Lehmann B, Leyer I (2011) Hydrological prerequisites for optimum habitats of riparian *Salix* communities - identifying suitable reforestation sites: Optimum habitats of riparian *Salix* communities. *Appl Veg Sci* 14:367–377. doi: 10.1111/j.1654-109X.2011.01121.x
- Mosner E, Weber A, Carambia M, Nilson E, Schmitz U, Zelle B, Donath T, Horchler P (2015) Climate change and floodplain vegetation—future prospects for riparian habitat availability along the Rhine River. *Ecol Eng* 82:493–511. doi: 10.1016/j.ecoleng.2015.05.013
- Nagelkerke NJD (1991) A note on a general definition of the coefficient of determination. *Biometrika* 78:691–692. doi: 10.1093/biomet/78.3.691
- Newbold C (1997) *Water level requirements of wetland plants and animals*. English Nature, Peterborough
- Pinheiro J, Bates D, DeBroy S, Sarkar D, R Core Team (2017) *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-131

- R Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria
- Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIOMOD – a platform for ensemble forecasting of species distributions. *Ecography* 32:369–373. doi: 10.1111/j.1600-0587.2008.05742.x
- Tockner K, Stanford JA (2002) Riverine flood plains: present state and future trends. *Environ Conserv* 29:308–330. doi: 10.1017/S037689290200022X
- Van Eck WHJM, Van De Steeg HM, Blom CWPM, 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. doi: 10.1111/j.0030-1299.2004.13083.x
- Vaughan IP, Ormerod SJ (2005) The continuing challenges of testing species distribution models. *J Appl Ecol* 42:720–730. doi: 10.1111/j.1365-2664.2005.01052.x
- Vervuren PJA, Blom CWPM, De Kroon H (2003) Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. *J Ecol* 91:135–146. doi: 10.1046/j.1365-2745.2003.00749.x
- Ward JV, Tockner K, Schiemer F (1999) Biodiversity of floodplain river ecosystems: ecotones and connectivity. *Regul Rivers Res Manag* 15:125–139. doi: 10.1002/(SICI)1099-1646(199901/06)15:1/3<125::AID-RRR523>3.0.CO;2-E
- Wickham H (2009) *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York

## Annex 4

**Table 4.A1** The 23 target species and indices used for the SDM.

Species	Burkart	RLS Hesse	DB presence	ELL F	ELL WF
<i>Achillea millefolium</i> L.	0	LC	95	4	0
<i>Agrimonia eupatoria</i> L.	0	LC	49	4	0
<i>Arabis nemorensis</i> (Hoffm.) W. D. J. Koch	1	EN	20	7	0
<i>Bromus racemosus</i> L.	0	VU	25	8	1
<i>Centaurea jacea</i> L.	0	LC	25	indifferent	0
<i>Galium boreale</i> L.	1	VU	14	6	1
<i>Inula salicina</i> L.	0	NT	23	6	1
<i>Iris pseudacorus</i> L.	0	LC	15	9	0
<i>Iris spuria</i> L.	0	VU	15	7	0
<i>Leucanthemum vulgare</i> (Vail.) Lam.	0	LC	51	4	0
<i>Linum catharticum</i> L.	0	LC	10	indifferent	0
<i>Lotus corniculatus</i> L.	0	LC	49	4	0
<i>Lysimachia vulgaris</i> L.	0	LC	21	8	1
<i>Peucedanum officinale</i> L.	1	VU	19	4	1
<i>Prunella vulgaris</i> L.	0	LC	43	5	0
<i>Ranunculus acris</i> L.	0	LC	64	6	0
<i>Rhinanthus alectorolophus</i> Pollich	0	NT	11	4	0
<i>Sanguisorba officinalis</i> L.	1	LC	57	6	1
<i>Serratula tinctoria</i> L.	0	EN	13	indifferent	0
<i>Silaum silaus</i> (L.) Schinz & Thell.	1	LC	30	indifferent	1
<i>Thalictrum flavum</i> L.	1	LC	16	8	1
<i>Veronica maritima</i> L.	1	VU	20	8	1
<i>Vincetoxicum hirsutaria</i> Medik.	0	LC	12	3	0

Burkart: classification as river corridor plant or floodplain meadow species (Burkart 2001); RLS Hesse: Red List status in Hesse (Hemm et al. 2008), Endangered = EN, Vulnerable = VU, Near Threatened = NT, Least Concern = LC; DB presence: species' presence in database (number of occurrences); ELL F: Ellenberg indicator value (EIV) for moisture (Ellenberg et al. 1991); ELL WF: EIV for alternating moisture conditions (Ellenberg et al. 1991). Species nomenclature followed Jäger (2017). In total, 226 vegetation plots served as a basis for habitat modeling; 78 vegetation plots (sampled 2011–2012) were taken from the KLIWAS project (Horchler et al. 2012) and 31 plots (sampled 2014) were derived from a resampling of restoration sites of the City of Riedstadt. To gain a spatially equaled number of plots over the whole study area we sampled 117 plots in 2015 and 2016. To avoid a modeling bias through spatial autocorrelation, we assured that the minimum distance between plots was higher than 50 m (Dormann et al. 2007).

**Table 4.A2** All a priori hydrological, meteorological and morphological predictors

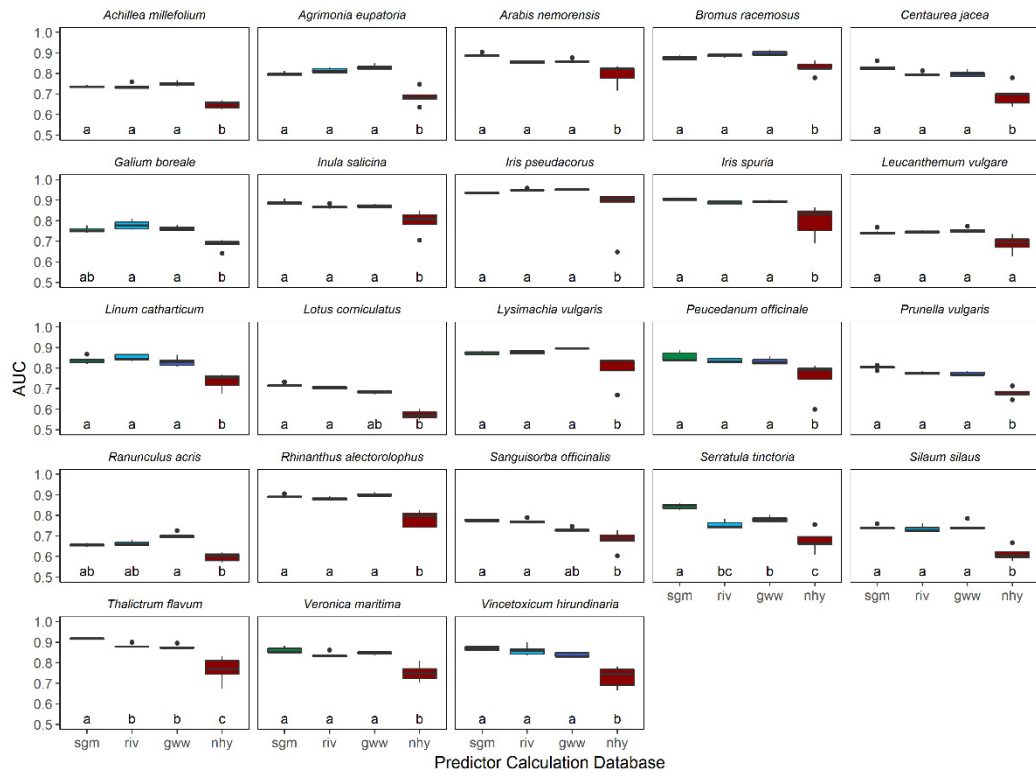
Nr.	Description of hydrological predictor
01	Mean of groundwater level (m)
02	Maximum of groundwater level (m)
03	Minimum of groundwater level (m)
04	Standard deviation of groundwater level (m)
05	Range of groundwater level (m)
06	Sum of days with inundation (days)
07	Longest inundation period (days)
08	Maximum height of inundation (m)
09	Day after start of growing season, on which longest inundation period starts (m)
10	Day of year, on which longest inundation period starts (m)
11–13	Sum of inundation days in the first 60, 80, 100 days after start of growing season (days)
14–16	Longest inundation period in the first 60, 80, 100 days after start of growing season (days)
17–23	Sum of days with groundwater level below 30, 50, 70, 100, 150, 200, 250 cm below ground (days)
24–30	Sum of days with groundwater level above 30, 50, 70, 100, 150, 200, 250 cm below ground (days)
31–37	Longest period with groundwater level below 30, 50, 70, 100, 150, 200, 250 cm below ground (days)
38–44	Longest period with groundwater level above 30, 50, 70, 100, 150, 200, 250 cm below ground (days)
45–52	Sum of days with inundation height more than 5, 10, 15, 20, 30, 50, 100, 150 cm (days)
53–60	Longest period with inundation height more than 5, 10, 15, 20, 30, 50, 100, 150 cm (days)
61–63	Sum of days with groundwater level below 50 cm below ground in the first 60, 80, 100 days after start of growing season (days)
64–66	Longest period with groundwater level below 50 cm below ground in the first 60, 80, 100 days after start of growing season (days)
67–69	Days with groundwater level below 50 cm below ground and precipitation < 1 mm in the first 60, 80, 100 days after start of growing season (days)
70–72	Days with groundwater level below 50 cm below ground and precipitation ≥ 1 mm in the first 60, 80, 100 days after start of growing season (days)
73–75	Longest period with groundwater level below 50 cm below ground and precipitation < 1 mm in the first 60, 80, 100 days after start of growing season (days)
76–78	Longest period with groundwater level below 50 cm below ground and precipitation ≥ 1 mm in the first 60, 80, 100 days after start of growing season (days)
79–81	Number of periods with inundation periods longer than 5, 7, 10 days

**Table 4.A2** continued

Nr.	Description of meteorological predictor
01	Sum of precipitation (mm)
02	Sum of wet days (Precipitation $\geq 1$ mm) (days)
03	Sum of dry days (Precipitation $< 1$ mm) (days)
04	Longest period of wet days (Precipitation $\geq 1$ mm) (days)
05	Longest period of dry days (Precipitation $< 1$ mm) (days)

Nr.	Description of morphological predictor
01	Height above NN (derived from the digital elevation model) (m)
02–03	Northness and Eastness
04–05	Northing and Easting
06	Distance to the Rhine River (m)
07	Distance to the Rhine or the meander cutoff (m)
08	Distance to any water surface (distance to Rhine or the meander cutoff or lake) (m)
09	Topographic wetness index



**Fig. 4.A1** Comparison of model quality (area under the receiver operating characteristic curve, AUC) of 4 different predictor calculation databases for species distribution models for 23 target species of floodplain restoration projects. Predictor calculation databases: surface-groundwater model, sgm; interpolated water level Rhine River data, riv; interpolated groundwater level data, gww; non hydrological, nhy. Letters denote significant differences of hydrological calculation method ( $p < 0.05$ ) according to ANOVA post hoc Tukey tests for each species.

#### **Additional references annex 4**

- Burkart M (2001) River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. *Glob Ecol Biogeogr* 10:449–468. doi: 10.1046/j.1466-822x.2001.00270.x
- Dormann CF, McPherson JM, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz W, Daniel Kissling W, Kühn I, Ohlemüller R, Peres-Neto PR, Reineking B, Schröder B, Schurr FM, Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30:609–628. doi: 10.1111/j.2007.0906-7590.05171.x
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulissen D (1991) Zeigerwerte von Pflanzen in Mitteleuropa (Indicator values of plants in Central Europe), 3rd edn. Goltze, Göttingen
- Hemm K, Frede A, Kubosch R, Mahn D, Nawrath S, Uebeler M, Barth U, Gregor T, Buttler KP, Hand R, Cezanne R, Hodvina S, Huck S (2008) Rote Liste der Farn- und Samenpflanzen Hessens (Red list of fern and seed plants in Hesse), 4th edn. Hessisches Ministerium für Umwelt, ländlichen Raum und Verbraucherschutz (HMULV), Wiesbaden
- Horchler P, Mosner E, Peper J (2012) AuVeg – a database of German floodplain vegetation. *Biodivers Ecol* 4:367–367. doi: 10.7809/b-e.00158
- Jäger EJ (ed) (2017) Rothmaler - Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband (Fieldflora of Germany, vascular plants, basic volume), 21st edn. Springer Spektrum, Berlin



## Abstract

Floodplain meadow plant species are particularly adapted to the specific environmental conditions (e.g., the interplay of flooding and drought) in the floodplains of Europe's large rivers. Numerous species of this set of species often jointly occur at floodplain grassland despite their ecological heterogeneity. The traits that cause the joint distribution pattern still have hardly been studied. This thesis deals with the flooding tolerance of selected floodplain meadow species with a focus on different key factors of floods. Furthermore, the spatial distribution of species based on (mainly hydrological) environmental variables was studied. Two experiments showed that increases in flooding duration, flooding depth and the combination of the two factors (i.e., intensity of the flooding effect) as well as the occurrence of a flooding event at young plant age (younger than ~4–6 weeks) result in severe limitation to seedling establishment. The combined effect of flooding duration and depth and often interactions in general have been underestimated in experimental studies so far. Hence, the results of these studies are difficult to compare. Using an interdisciplinary approach (disciplines: hydrology and ecology) a habitat model of 23 floodplain meadow species was developed. The species distribution was modeled by relating occurrence of species to several environmental variables (i.e., morphological, meteorological, hydrological). The hydrological predictor variables (e.g., flooding depth and duration) were generated from a hydrological model, which simulates the surface water-groundwater interactions with a high temporal resolution. Habitat models that include hydrological parameters from the hydrological model show better results for floodplain meadow species' distribution than models based on simple hydrological parameters. Habitat-suitability maps based on the habitat modeling were computed for the 23 target species. These maps could serve as a baseline for the target site selection of upcoming restoration projects (e.g., the reestablishment of typical floodplain meadow species). That enables an estimation of the restoration success in advance. Consequently, false investments of limited resources (e.g., freshly-cut, seed containing plant material, financial resources) through the restoration on unsuitable sites can be prevented.

## Zusammenfassung

Stromtalpflanzen sind ideal an die Umweltbedingungen in den Auen der großen Ströme Europas (z. B. das Wechselspiel aus Überflutung und Trockenheit) angepasst. Viele Arten aus dieser Artengruppe kommen meistens gemeinsam auf den Auenwiesen vor, sind jedoch ökologisch überaus heterogen. Die Eigenschaften, die das gemeinsame Verbreitungsmuster erklären, sind noch weitgehend unerforscht. Die vorliegende Dissertation behandelt zum einen die Überflutungstoleranz von ausgewählten Stromtalpflanzen mit Fokus auf unterschiedlichen Faktoren und zum anderen die räumliche Verteilung der Arten auf Basis von insbesondere hydrologischen Umweltvariablen. Mit zwei Experimenten wurde gezeigt, dass eine längere Überflutungsdauer, eine höhere Überflutungshöhe und die Interaktion der beiden Faktoren (d. h. Intensität des Überflutungseffektes) sowie das Auftreten einer Überflutung bei geringem Alter der Pflanzen (jünger als ca. 4–6 Wochen) in starker Einschränkung der Jungpflanzenentwicklung resultiert. Der kombinierte Effekt aus Überflutungsdauer und -höhe bzw. Interaktionen generell, wurden in vielen experimentellen Studien bisher unterschätzt und diese leiden daher an fehlender Vergleichbarkeit. Anhand eines interdisziplinären Ansatzes aus Hydrologie und Ökologie wurde eine Habitatmodellierung von 23 Stromtalpflanzen erstellt. Das Vorkommen der Pflanzenarten wurde basierend auf verschiedenen Umweltvariablen (morphologischer, meteorologischer und hydrologischer Variablen) modelliert. Die hydrologischen Prädiktorvariablen (z. B. Überflutungshöhe und -dauer) wurden aus zeitlich hochaufgelösten Simulationen eines hydrologischen Modells, das die Interaktion zwischen Oberflächenwasser und Grundwasser darstellt, abgeleitet. Habitatmodelle, die hydrologische Variablen berücksichtigen, die aus dem hydrologischen Modell abgeleitet wurden, können die Artenverteilung von Stromtalpflanzen besser erklären als Modelle, die stark vereinfachte hydrologische Variablen enthalten. Auf Basis des Habitatmodells wurden Habitateignungskarten für die 23 Stromtalpflanzen erstellt. Diese Karten können zukünftig als Grundlage für eine Flächenauswahl bei Renaturierungsprojekten zur Wiederansiedlung der typischen Stromtalpflanzen dienen. Der Renaturierungserfolg kann dadurch besser abgeschätzt werden und Fehlinvestitionen (z. B. von begrenzt zur Verfügung stehendem Mahdgut bzw. finanziellen Mitteln) durch eine Renaturierung an ungeeigneten Standorten, können dadurch minimiert werden.

## Acknowledgments

Many people have helped to enable this thesis and I thank all of them. In particular, I thank Prof. Dr. Dr. habil. Dr. h. c. (TSU) Annette Otte for giving me the opportunity to work on this interesting topic in her working group, for the professional and pleasant working environment, and for her trust in the last years. Special thanks go to Prof. Dr. Volkmar Wolters for his willingness to be the second supervisor of this thesis. I thank all colleagues and former colleagues at the Division of Landscape Ecology and Planning for the friendly working atmosphere and fruitful discussions, especially Dr. Sarah Harvolk-Schöning, Dr. Kristin Ludewig, PD Dr. Tobias W. Donath, as well as Josef Scholz-vom Hofe for his invaluable help with the experiments. I also thank the colleagues of the Division of Landscape, Water and Biogeochemical Cycles, in particular Nadine Maier, for the great collaboration in the project. Thanks go to the City of Riedstadt (Matthias Harnisch) and HessenForst (Ralph Baumgärtel) for data provision and support during fieldwork. I thank all contributors of vegetation data for their willingness to share datasets, i.e., the KLIWAS project group, and the City of Riedstadt and Dr. Dorota Michalska-Hejduk. Furthermore, I thank the Regierungspräsidium Darmstadt for issuing the permits for the fieldwork. Thanks go to Prof. Dr. Bernhard Höfle (Heidelberg University) for lending the RTK GNSS device. I acknowledge the Deutsche Bundesstiftung Umwelt for funding of the research project (Project No. 31612/01) and the Bundesanstalt für Gewässerkunde, the Hessisches Landesamt für Naturschutz, Umwelt und Geologie, and the Hessisches Landesamt für Bodenmanagement und Geoinformation for data provision. Finally, I am thankful to my family and friends for all their support and for the happiness they bring to my life.

## Declaration

I declare that I have completed this dissertation single-handedly without the unauthorized help of a second party and only with the assistance acknowledged therein. I have appropriately acknowledged and cited all text passages that are derived verbatim from or are based on the content of published work of others, and all information relating to verbal communications. I consent to the use of an anti-plagiarism software to check my thesis. I have abided by the principles of good scientific conduct laid down in the charter of the Justus Liebig University Giessen “Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis” in carrying out the investigations described in the dissertation.

Giessen, 19. July 2018

Johannes P. Gattringer