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**GERMINATION, ESTABLISHMENT AND DISTRIBUTION OF  
HARDWOOD FLOODPLAIN FOREST SPECIES**

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## List of publications

This dissertation is based on the following three articles:

1. Schindler, M., Terwei, A., Donath, T.W., Ludewig, K. (submitted manuscript). Three hardwood floodplain forest species experience different flooding durations inside and outside a dike relocation area at the Elbe River.
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3. Schindler, M., Schäfer, F., Donath, T.W., Ludewig, K. (2021). No evidence for flooding stress memory in saplings of eight hardwood floodplain forest species. Plant Ecology. doi:10.1007/s11258-021-01120-w.

### Author contributions:

For all three of the articles, Kristin Ludewig, Tobias W. Donath and me had the main responsibility for conceptualization. Further, I took the main responsibility for data analysis and paper writing and conducted most of the fieldwork and experimental work for the three studies. Lisa Jungmann helped me with data collection in the second study and Franziska Schäfer in the third study. All co-authors gave helpful comments and suggestions to improve the manuscripts.

# **Chapter 1**

Synthesis

Germination, establishment and distribution of  
hardwood floodplain forest species

# Introduction

## *Hardwood floodplain forests*

Floodplains are the areas adjacent to rivers that are influenced by fluctuating water levels, leading to an alternation of flooding and drought (Schwartz, 2001). They form the transitional zone between aquatic and terrestrial ecosystems (Richardson et al., 2007) and belong to the most productive and species-rich ecosystems, both in Central Europe and also worldwide (Brunotte et al., 2009; Tockner & Stanford, 2002). Generally, the vegetation of floodplains can be divided into different zones with increasing distance from the river (Ellenberg & Leuschner, 2010). The areas directly adjacent to the river are dominated by fast-growing annual species that will be gradually replaced by reeds at lower reaches (Ellenberg, 2009). With increasing distance from the river, softwood floodplain forests are found, being replaced by hardwood floodplain forests at higher elevations, where flooding events are shorter and less frequently (Siebel & Bouwma, 1998).

Due to anthropogenic interventions during the last centuries, like the expansion of rivers and navigable waterways as well as the use of floodplains as areas for settlements and agriculture, today they are among the most threatened habitats in Germany (Colditz, 1994; Glaeser et al., 2009). In addition to the pure loss of area of the recent (i.e. actively flooded) floodplain through dikes (Brunotte et al., 2009), a change in the runoff regime and a reduction in the hydro- and morphodynamics of the river through watercourse shortening, straightening and the construction of structures such as dams, barrages, bank reinforcement and groynes are responsible for this (Brunotte et al., 2009; Ward & Stanford, 1995). According to the floodplain status report for Germany, only 10–20% of the former floodplains are left in many sections of the major German rivers (Brunotte et al., 2009). Ecologically functional floodplains make up less than 10% and near-natural hardwood floodplain forests even only about 1% of the recent floodplains (Brunotte et al., 2009). This is particularly serious because hardwood floodplain forests are one of the most structure- and species-rich forest ecosystems in Central Europe (Naiman et al., 1993; Tockner & Stanford, 2002). Further, they harbour numerous rare and endangered species (Naiman et al., 1993). In addition to their ability to provide a variety of different habitats, they also offer several valuable ecosystem services, such as climate protection (carbon sink; Shupe et al., 2021), human recreation as well as water and nutrient retention (Weiß & Peterson, 2001).

### *The importance of flooding*

Under natural conditions, the zonation of woody species in floodplains is mainly determined by the hydrological regime (Blom & Voeselek, 1996). The water level of the river affects the vegetation both directly through flooding as well as indirectly through the balance of soil and groundwater. The water balance in the corresponding area is therefore of central importance for the explanation of the small-scale changes of different plant communities (Kozłowski, 2002). However, flooding frequency and duration not only influence the soil water balance but also the gas balance, the input of nutrients and pollutants, as well as sedimentation and erosion processes (Ellenberg, 2009). Therefore, even minor variations in flooding frequency and duration can lead to distinct differences in species composition (Kozłowski, 2002).

In general, flooding causes sustainable stress for terrestrial plants. The main problem during flooding is the shortage of oxygen due to the slow diffusion rates of gases in water (Glenz et al., 2006). A reduction in oxygen availability in the rhizosphere reduces not only the absorption of oxygen, but also negatively affects water and macronutrient uptake (Du et al., 2012), which can lead to reduced growth, a high injury level or even death (Mommer & Visser, 2005). However, not all plant species are equally vulnerable to flooding (Bockelmann et al., 2002; Lenssen et al., 1999; Silvertown et al., 1999; Sýkora et al., 1988). Differences can be explained by the ability to react to resulting stress in morphological, physiological and metabolic terms. Thus, species that grow in such habitats must be adapted to flooding in some way (Leyer, 2004; Mountford & Chapman, 1993). One of the most common adaptations of woody plants to flooding is the ability to form morphological structures, such as hypertrophied lenticels, aerenchyma tissues and adventitious roots (Glenz et al., 2006). Those structures increase the uptake of oxygen and promote its transportation into the root system (Du et al., 2012). Therefore, flooding tolerance can be regarded as a key factor for the successful colonization of plant species in floodplains (Glenz et al., 2006; Streng et al., 1989).

Unfortunately, the knowledge of flooding tolerance particularly of hardwood floodplain forest species is still sparse and in many cases contradictory, as it depends on several influencing factors (Glenz et al., 2006). Regarding the factor flooding depth, it is important to make distinction between complete inundation (total submergence), partial inundation and soil saturation. In terms of flooding frequency, the time since last flooding is the most decisive factor influencing flooding tolerance (Glenz et al., 2006). Nevertheless, the determining factor for the location of the transitional vegetation zone between softwood and hardwood floodplain

forests is solely the flooding duration (Ellenberg, 2009). The softwood floodplain forest species at the lower Middle Elbe tolerate a flooding duration of 120–197 days/year, the transitional zone between softwood and hardwood floodplain forest species is assigned by 86–119 days/year and hardwood floodplain forest species tolerate 1–85 flooding days/year (Pott, 2000). Furthermore, the hardwood floodplain forest can be separated in higher and lower lying sites (Michiels & Aldinger, 2002). However, these are schematic classifications, as the zones often merge into each other under natural conditions. Generally, the longer trees are exposed to flooding, the greater the injury level (Blom & Voeselek, 1996; Toner & Keddy, 1997). In addition to flooding frequency, depth or duration, seasonal timing is another decisive factor, as flooding often has little or no effect during the winter season, but can severely affect plants growth and survival during the growing season due to a higher metabolic activity (Kozłowski, 1997; Siebel & Blom, 1998). Further, stagnant water is more harmful to plants than flowing water (Frye & Grosse, 1992). The reason is a lower oxygen concentration due to the lack of water layer mixture as well as a reduced decomposition of plant material, leading to altered chemical compounds compared to flowing water (Glenz, 2006). Gorzelak (2000) observed for the 4-week flood at the river Oder in Poland in 1997, that *F. excelsior* and *A. pseudoplatanus* suffered more in sites with stagnant water, but less in sites under flowing water. Furthermore, also the developmental stage of the plants is crucial for their flooding tolerance (Glenz et al., 2006; Kozłowski, 1997; Siebel & Blom, 1998). Within the process of natural regeneration of tree species, the phase of sapling establishment is highly important because this stage is the most vulnerable period in the life cycle of the individual tree (Cavers & Harper, 1967; Marks & Prince, 1981). Adult trees tolerate flooding better than saplings of the same species (Gill, 1970; Hall & Smith, 1955; Kozłowski, 1997; Siebel & Blom, 1998). Thus, even those species rated as flooding-tolerant may be quite sensitive in the seedling stage (Glenz et al., 2006). Consequently, knowing the species requirements during their establishment phase has important implications for planning and design of restoration measures (Bobic, 2012; Liira et al., 2011).

### *Restoration of floodplain forests*

Due to the importance of hardwood floodplain forests, research and nature conservation projects are increasingly focusing on the restoration of floodplains and, in particular, on the possibilities to re-establish hardwood floodplain forests (Finck et al., 2002). Nevertheless, the implementation of restoration measures for these highly dynamic ecosystems is a challenging task. Up to now, little is known about successional processes of floodplain forests. This is



mainly due to the lack of long-term monitoring programs and because hardwood stands take a long time, usually 100–150 years, to develop again at sites that correspond to a near-natural floodplain forest with their typical vegetation composition and stand structure (Bierhals et al., 2004; Scholz et al., 2012). Although the Elbe has also been heavily modified by humans in recent centuries, it is still one of the most natural large rivers within Central Europe (Scholz, 2005). Large parts of the active floodplain in the entire Elbe basin are included in the European protected area system “Natura 2000” according to the Habitats Directive (Scholz, 2005). Due to the closeness to nature, these protected areas are particularly well suited for restoration projects, aiming at the regeneration of hardwood floodplain forests.

One of the most effective methods to restore hydrologically dynamic floodplains is to re-expose them to periodical flooding by removing or relocating the existing dikes. At the time of dike relocation, the hydrologically reconnected areas are usually dominated by arable fields or cultivated grassland and thus host plant communities that have not been exposed to flooding for a long time or even never. Consequently, secondary succession will start after changing the hydrological regime. This means that new species communities, better adapted to the new conditions will gradually replace the existing ones.

In restoration projects, trees are often planted to support and speed up the natural processes, because hardwood floodplain forest succession processes need several decades up to centuries to run (Mosner et al., 2009). Nonetheless, even planted trees can show a high mortality, as this was the case in one of the largest dike relocation areas in Germany near the city of Lenzen (Purps, 2016). Unfortunately, in many cases, the effects and the success of restoration projects on biodiversity and species composition are still widely unknown, as only few projects were monitored and almost no long-term monitoring programs exist (Schneider et al., 2017). However, particularly with regard to the assessment of the long-term success of future restoration measures, this knowledge is of high importance (Schneider et al., 2017).

To summarize, all the mentioned factors above are decisive for the zonation and differentiation of plant communities inside floodplain ecosystems. The complex interactions between physical and biological processes in floodplains make restoration efforts even more difficult (Rood et al., 2003). Therefore, successful restoration is based on the knowledge and consideration of the ecological, hydrological and geomorphological processes (Glenz et al., 2006). A better knowledge about flooding tolerance as well as the determining factors would improve the chances of success of implemented riparian forest restoration measures. Due to the complexity

of the dynamic processes in floodplains, it is not beneficial to consider all these parameters simultaneously, as they probably would distort the individual factor. This is why this thesis mainly focuses on flooding duration, being the most decisive factor to differentiate the zonation of floodplain forests (Ellenberg, 2009). Nevertheless, it is important to combine experimental studies, where it is possible to control the hydrological conditions, with field experiments, where the hydrological regime as well as other influencing factors are unpredictable, in order to not neglect the interaction of all these factors. Therefore, in this dissertation, controlled common garden experiments were combined with field experiments to assess to what extent the flooding duration under natural conditions is crucial for hardwood floodplain forest establishment as well as to obtain a better knowledge of the interacting processes in floodplain restoration areas.

## Objectives

With the previous statements, the importance of alluvial forests for biodiversity and therefore the importance for their conservation and restoration as essential goal for nature conservation projects in river landscapes were presented comprehensively. As one of the first and largest completed dike relocation projects in Germany, with the objective of restoring alluvial forests, the dike relocation “Lenzen-Wustrow” is of particular importance and has a special pilot character for similar projects in the future (Damm, 2013). Due to the complex and unpredictable hydrodynamics in floodplains, the success of such projects is difficult to predict and for example, in case of the dike relocation “Lenzen-Wustrow”, has often resulted in high mortality of planted trees. To enhance the success of future restoration projects, hydrological factors such as the influence of flooding duration on the establishment of hardwood floodplain forest species has to be investigated in more detail. To this end, this dissertation aims to gain a better understanding of flooding tolerance patterns, focusing on the tolerance to flooding duration of different hardwood floodplain forest species. It combines controlled common garden experiments with field experiments inside the dike relocation area “Lenzen-Wustrow”.

In particular, this dissertation focuses on the following objectives:

1. Comparison of the elevational occurrence and thus the experienced flooding duration of individuals of different hardwood floodplain forest species inside the dike relocation

area with individuals of the same species occurring within the surrounding active floodplain (field study; chapter 2).

2. Influence of flooding duration and aeration on the establishment of saplings of different hardwood floodplain forest species (experimental study; chapter 3).
3. Analysis of the role of repeated flooding events on the overall flooding tolerance of juveniles of different hardwood floodplain forest species (experimental study; chapter 4).

## Study area

The study area is located about halfway between the cities of Berlin and Hamburg in the border zone of the two German federal states of Brandenburg and Lower Saxony (Fig. 1.1A). It is part of the lower Middle Elbe River section and includes the dike relocation area “Lenzen-Wustrow” and the adjacent floodplain zone between Elbe-km 438.60 and 495.95. This area refers also to the Biosphere Reserve Elbe River Landscape and is a site of pan-European importance according to the European Habitats Directive (LfU, 2017). The Middle Elbe region belongs to a transitional climate zone and is influenced by the sub-Atlantic north-western German lowlands and the sub-continental regions of eastern Central Europe (Miest, 1972). For the years 1995–2017, an average annual temperature of 9.7 °C and a mean annual precipitation of 607 mm was recorded (DWD, 2018). The discharge of the Elbe is closely related to the climatic and geomorphological conditions of its catchment area, and thus shows characteristic pronounced winter and spring floods with beginning of snow melt in the Czech Giant Mountains. Summer floods are rather rare (Leyer, 2002). The study area is characterized by fluvial sediments that form layers of different soils. The largest proportion consists of alluvial loams, which contain sandy, silty or clayey fractions that have accumulated depending on the flooding conditions (Schwartz, 2001).

The dike relocation area “Lenzen-Wustrow” is part of a national major conservation project in which between 2002 and 2011 420 ha of hydrological floodplain was reconnected to the hydrodynamics of the Elbe River (Fig. 1.1B). This was implemented by a new dike up to 1.3 km inland and the old dike’s opening by six breaches (Damm, 2013). To initiate and speed up the

development of alluvial forest inside the area, trees were planted on 77 ha of grassland from 2004 to 2008. Additionally, independent from the dike relocation, an afforestation covering 65 ha, was already realized in 1996 (Damm, 2013). Due to its physical barriers, numerous flood channels and depressions, the area is characterized by a specific and complex morphology and hydrodynamic (Faulhaber et al., 2013). The actual vegetation presents a mosaic of fallow grasslands, alluvial grasslands, forb communities, and alluvial forests (Damm, 2013). The alluvial forests in the study area are characterized by three main association types: the *Salicetum triandro-viminalis* and *Salicetum albae*, consisting of softwood floodplain forest species such as the shrubs *Salix purpurea*, *S. viminalis*, *S. triandra* and the trees *S. alba*, *S. fragilis* and *Populus nigra*. The *Quercus-Ulmetum* is dominated by the hardwood floodplain forest elements *Quercus robur* and *Ulmus laevis* in the tree layer as well as *Crataegus monogyna* and *Cornus sanguinea* in the shrub layer.

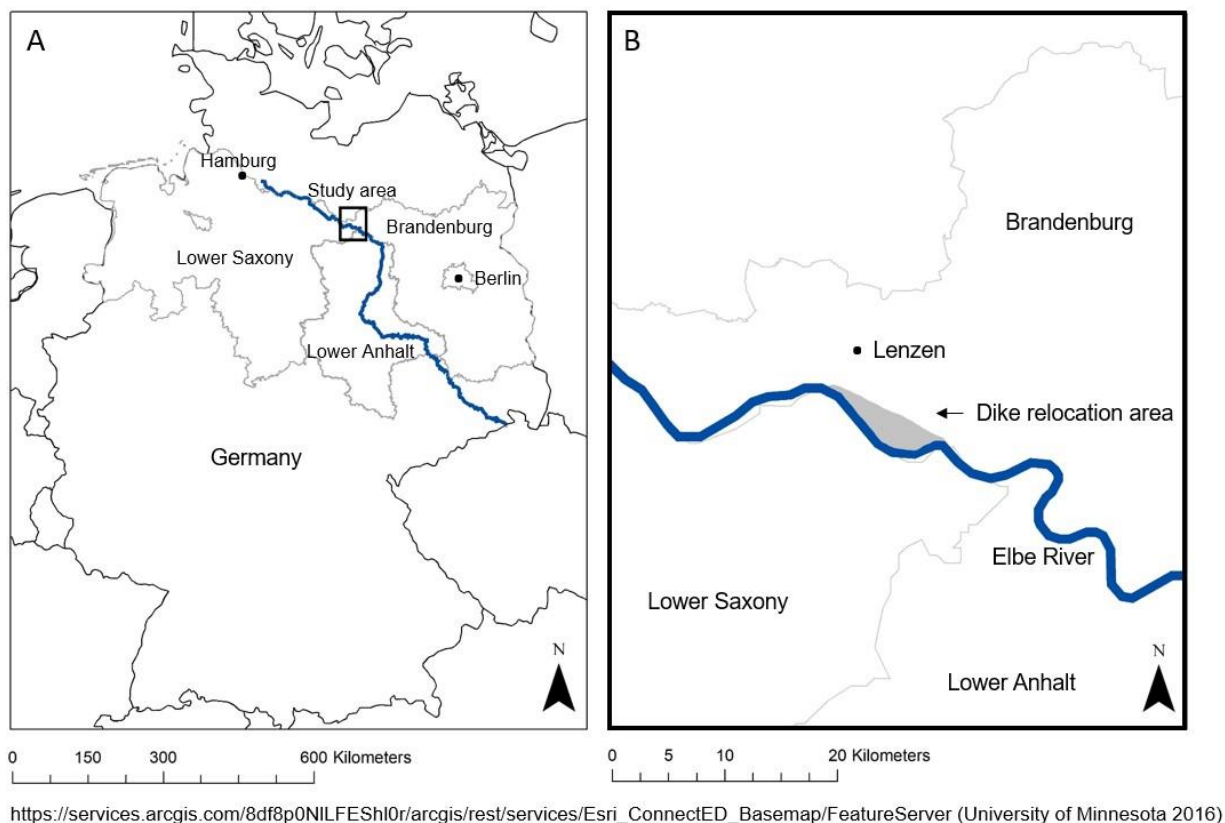


Fig 1.1 Geographical location of the study area in Germany (A), and overview of the study area including the dike relocation area and surroundings (B).

The common garden experiment of this dissertation (chapter 3 and 4), was set up at the research station “Linden-Leihgestern” of the Justus-Liebig University (Giessen, Germany, 50° 32’ N, 8° 41’ E). However, seed sampling for both studies was conducted in the previously described

study area within the range of NW 53° 21' N, 10° 42' E and SE 52° 58' N, 11° 38' E), both, inside the active and the fossil floodplain along the lower Middle Elbe River.

## Chapter outline

This dissertation is based on three manuscripts (chapter 2, 3 and 4). All of them have been submitted to international peer-reviewed scientific journals. The manuscripts in chapter 3 and 4 are already published, whereas the manuscript in chapter 2 is currently under peer-review. The studies in chapter 3 and 4 were carried out under controlled common garden conditions, while the study of chapter 2 was conducted inside an alluvial restoration area under natural field conditions. The different chapters all deal with different aspects of flooding tolerance of typical hardwood floodplain forest species (Tab. 1.1).

Tab. 1.1 Information about study species, their family, habitus (T = tree, S = shrub), site preference (LH = lower lying hardwood floodplain; HH = higher lying hardwood floodplain, classification followed Michiels & Aldinger, 2002) and their usage in the studies (C2 = chapter 2, C3 = chapter 3, C4 = chapter 4). The nomenclature followed Rothmaler et al., 2017.

Species	Family	Habitus		Preference		Usage		
		T	S	LH	HH	C2	C3	C4
<i>Acer negundo</i> L.	Sapindaceae	X		X			X	X
<i>Acer pseudoplatanus</i> L.	Sapindaceae	X			X		X	X
<i>Cornus sanguinea</i> L.	Cornaceae		X	X			X	X
<i>Crataegus monogyna</i> JACQ.	Rosaceae		X	X		X	X	X
<i>Fraxinus excelsior</i> L.	Oleaceae	X		X			X	X
<i>Fraxinus pennsylvanica</i> MARSHALL	Oleaceae	X		X			X	X
<i>Quercus robur</i> L.	Fagaceae	X		X		X	X	X

		Habitus		Preference		Usage		
Species	Family	T	S	LH	HH	C2	C3	C4
<i>Quercus rubra</i> L.	Fagaceae	X					X	
<i>Sambucus nigra</i> L.	Adoxaceae		X		X		X	X
<i>Sorbus aucuparia</i> L.	Rosaceae	X	X		X		X	
<i>Ulmus laevis</i> PALL.	Ulmaceae	X		X		X		

A brief outline of the contents and applied methods of each study follows, while the main results and conclusions will be discussed in the subsequent section.

**Chapter 2** Three hardwood floodplain forest species experience different flooding durations inside and outside a dike relocation area at the Elbe River.

This manuscript deals with the comparison of the occurrence of individuals of three hardwood floodplain forest species (*U. laevis*, *Q. robur*, *C. monogyna*) inside a dike relocation area “Lenzen-Wustrow”, where most trees were planted as part of an alluvial restoration project with individuals of the same species occurring in the surrounding active floodplain. The fieldwork was carried out in August 2017 and 2018. For this purpose, the position of each individual of the target species ( $\geq 2$  m height) was recorded within prior defined transects inside and outside the dike relocation area. Altogether, 2,516 individuals were recorded (1,166 of *U. laevis*, 853 of *Q. robur* and 497 of *C. monogyna*). Subsequently, the relative elevation above Elbe mean water level and the corresponding number of flooding days for the entire year and for the growing season as mean value for the years 2011–2017 were calculated. I analysed differences in relative elevation and number of flooding days between species, location (inside versus outside the dike relocation area) and its interactions by conducting linear mixed-effect models (LMM).

**Chapter 3** Influence of flooding duration and aeration on saplings of ten hardwood floodplain forest species.

In this manuscript, the effects of flooding duration in combination with oxygen supply of the floodwater through aeration on six-week-old saplings of ten hardwood floodplain forest species was investigated in flooding basins. The species includes seven tree species *A. negundo*, *A. pseudoplatanus*, *F. excelsior*, *F. pennsylvanica*, *Q. robur*, *Q. rubra*, *S. aucuparia* as well as three shrub species *C. sanguinea*, *C. monogyna* and *S. nigra*. Both flooding-tolerant (*A. negundo*, *F. excelsior*, *F. pennsylvanica*, *Q. robur*, *C. sanguinea*, *C. monogyna*) and flooding-intolerant species (*A. pseudoplatanus*, *Q. rubra*, *S. nigra*, *S. aucuparia*) as well as native (*A. pseudoplatanus*, *F. excelsior*, *Q. robur*, *C. sanguinea*, *C. monogyna*, *S. nigra*, *S. aucuparia*) and non-native species (*A. negundo*, *F. pennsylvanica*, *Q. rubra*) were included (Tab. 3.1). Species selection was done in order to assess the suitability (natives) and propagation risk (non-native) of the investigated species in the context of restoration projects of hardwood floodplain habitats. Therefore, the saplings were exposed to partial flooding of three durations (three, six and nine weeks) and two oxygen levels (aerated and not aerated). Altogether, 490 plants were studied (10 plant species x 4 flooding durations (3 flooding durations and 1 unflooded control) x 2 oxygen levels (only 1 oxygen level for control) x 7 replications). I recorded foliar injury levels according to self-created classes and growth parameters in terms of plant height, number of leaves and stem diameter twelve weeks after the start of the experiment, including a recovery period of at least three weeks for the long flooding duration. Additionally, foliar injury was recorded again one year after the start of the experiment, including a recovery period of nine months. To analyse the effects of flooding duration, oxygen supply by aeration and their interaction on foliar injury and growth parameters, non-parametric Scheirer-Ray-Hare-tests and ANOVAs for split-plot designs were used.

**Chapter 4** No evidence for flooding stress memory in saplings of eight hardwood floodplain forest species.

This manuscript represents a study that built on the previous experiment of chapter 3 and investigated the possibility of saplings forming a flooding stress memory after recurrent flooding. To this end, the influence of a previous flooding on the flooding tolerance of fourteen-months-old saplings from eight hardwood floodplain forest species (*A. negundo*, *A. pseudoplatanus*, *F. excelsior*, *F. pennsylvanica*, *Q. robur*, *C. sanguinea*, *C. monogyna*, *S. nigra*) after a recurrent flooding was examined in flooding basins (Tab. 4.1). The individuals of the experiment already experienced a partial flooding of three durations (three, six or nine weeks) or no flooding during the previous year (chapter 3). After a nine-month recovery period under optimal garden conditions, they were again exposed to either nine weeks of partial

flooding or no flooding (Fig. 4.1). Foliar injury and growth parameters in terms of plant height, number of leaves and stem diameter were documented three weeks after flooding (short-term recovery). Foliar injury was additionally recorded nine months after flooding (medium-term recovery). Finally, to analyse the effects of the previous flooding, its duration, the new flooding treatment and their interactions on foliar injury, non-parametric Scheirer-Ray-Hare-tests were calculated. For differences in growth parameters, separate split-plot ANOVAs were conducted.

## Main results and conclusions

### *The effects of flooding and its duration*

In general, hardwood floodplain forest species are known to be adapted to withstand the special conditions they are exposed to during flooding events, at least for a certain period of time (Glenz et al., 2006). Nevertheless, most species (*A. pseudoplatanus*, *F. excelsior*, *Q. robur*, *Q. rubra*, *C. sanguinea*, *C. monogyna*, *S. nigra*, *S. aucuparia*) suffered from the effects of flooding, resulting in an increased mortality and injury level as well as reduced growth. I showed that an increasing flooding duration negatively affects plants performance in terms of survival and injury (chapter 3). Similar tolerance patterns were identified after a recurrent flooding event (chapter 4). However, *A. negundo*, *A. pseudoplatanus*, *F. excelsior*, *F. pennsylvanica*, *Q. robur*, and *C. monogyna* were able to recover better after a nine-month recovery period compared to the previous flooding experiment (chapter 3 and 4).

The negative effects of flooding on plants are mainly the result of a lack of oxygen in the root system (Bailey-Serres & Voesenek, 2008). This in turn can lead to an interruption or inhibition of essential physiological and metabolic processes (Glenz et al., 2006), such as lower photosynthesis rates that reduces the supply of essential assimilates (Colmer & Voesenek, 2009). As the duration of flooding increases, also the depletion of carbohydrate reserves increases, leading to cell damage caused by energy deficiency (Bailey-Serres & Voesenek, 2008). In order to avoid these conditions, plants developed several adaptive mechanisms (Colmer & Voesenek, 2009; Striker, 2012a). The most common ones are the formation of hypertrophied lenticels, aerenchym tissues and adventitious roots, which facilitate oxygen uptake and transportation from shoots to roots (Du et al., 2012). Whether, how quickly and how many of such adaptations are developed depends on the species and mainly determines their flooding tolerance.



Since the studied hardwood floodplain forest species react with different responses to flooding, it is not surprising that they show different degrees of flooding tolerance. *S. aucuparia*, for example, is not able to develop any of these morphological adaptations at all and therefore suffers most (chapter 3; Glenz et al., 2006). Further, *C. sanguinea* is only capable of forming adventitious roots, while *F. excelsior* L. and *Q. robur* can additionally form lenticels and aerenchyma (Frye & Grosse, 1992; Kozłowski, 1997; Siebel, 1998). This explains the lower mortality and injury level of *F. excelsior* and *Q. robur* compared to *C. sanguinea* for both experiments (chapter 3 and 4). Likewise, it is also crucial how quickly the structures can be formed, due to the fact that stomatal closure is one of the earliest responses to flooding for a number of species and stomata will only open again when hypertrophied lenticels and adventitious roots appear (Du et al., 2012; Kozłowski, 1997). The best performing species in both experimental studies were *A. negundo* and *F. pennsylvanica* that develop lenticels and adventitious roots immediately when flooded (chapter 3 and 4; Brink, 1954; Tang & Kozłowski, 1984), while most of the other studied species are not able to adapt that quickly and sometimes even need weeks (Colmer & Voeselek, 2009). In addition, also the number of the individual structure seems to play an important role. Colin-Belgrand et al. (1991) observed that both *Q. robur* and *Q. rubra* developed lenticels and adventitious roots, but *Q. robur* showed a significantly higher number of lenticels and adventitious roots, and therefore explains the better performance compared to *Q. rubra* in both experimental studies (chapter 3 and 4). Therefore, it can be assumed that the species that are able to quickly form different structures in a large number will cope better, even with long periods of flooding.

When investigating the growth parameters of the studied species, it can be concluded that it is highly important to consider them in conjunction with other plant performance parameters when estimating flooding tolerance. Species may respond with a similar behavior regarding growth, but with different effects on the specific species. For example, it is known that some species, such as seedlings of *Veronica maritima* (Gattringer et al., 2017), *Allium angulosum*, *Silaum silaum* and *Selinum carvifolia* (Gattringer et al., 2018), but also adult plants of the legume *Lotus tenuis* (Striker et al., 2011) and the weed *Rumex palustris* (Voeselek et al., 2006) are able to continue growing during flooding as strategy to rapid emerge leaves above water level. This seems to be particularly important under partial flooding (Striker, 2012b). Although the investigated species in both experimental studies were only partially flooded, this behavior was not observed, probably because the investigated species are in general characterized by slow growth (chapter 3 and 4). Another growth response during flooding is to temporarily suspend growth by slowing down the metabolism, thus saving energy and maintaining high

carbohydrate reserves (Blom et al., 1994; Frye & Grosse, 1992; Striker, 2012b; Tang & Kozlowski, 1984). This behavior have been found in *Ranunculus repens* (Lynn & Waldren, 2003), *Rumex crispus* (Voeselek & Blom, 1989), and seedlings of *Lotus tenuis* (Striker et al., 2012c), *Veronica teucrium* (Gattringer et al., 2017) and *Sanguisorba minor* (Gattringer et al., 2018). Regarding the study in chapter 3, this adaptive strategy was assumed for *F. excelsior* and *Q. robur*. Also *A. pseudoplatanus* and *Q. rubra* showed suspended growth but at the same time a high degree of injury. However, it can be concluded that the behavior of the latter two species is more likely to be classified as suffering (chapter 3). Similar conclusions can be derived when assessing the number of leaves. I showed that a reduction of leaves could be either an adaptive strategy or an indicator for suffering. The first strategy was observed for *C. monogyna* (chapter 3 and 4) and could be explained by reducing energy consumption. Consequently, new leaves will sprout as soon as environmental conditions become better (Mommer and Visser, 2005; Pires et al., 2018). The latter applies to *Q. rubra* and *C. sanguinea*, due to a high injury level in both experimental studies (chapter 3 and 4). Further, an increased stem diameter is observed for the species that could form aerenchym or lenticels due to the enlarged intercellular spaces (Frye & Grosse, 1992; Kozlowski, 1997; Roloff, 2010). This was particularly the case for *F. excelsior* and *F. pennsylvanica* (chapter 3 and 4), but also the stem diameter of the flooded individuals of *S. nigra* increased significantly, compared to the unflooded control (chapter 3). Nevertheless, this species suffered very badly later on (chapter 3), as explained in the subsequent paragraph. Therefore, growth parameters alone cannot provide sufficient information about flooding tolerance patterns of a species and should always be considered in conjunction with other performance parameters such as vitality or injury.

#### *The importance of a recovery period*

Both flooding experiments emphasize that it is highly important to assess the flooding tolerance of species also after a certain recovery period (chapter 3 and 4). For example, all individuals of *S. nigra* survived flooding with only low injury level, three weeks after flooding. In contrast, nine month after flooding, mortality and injury level was high although optimal garden conditions in the meantime were despite (chapter 3). In the first flooding experiment, *A. pseudoplatanus*, *F. excelsior*, *Q. robur* and *Q. rubra* showed a higher injury level after a nine-month recovery period compared to three weeks after flooding (chapter 3). When plants return from anaerobic to aerobic conditions after flooding, further stress factors can lead to even greater damage than during flooding (Blohkina et al., 2003; Striker, 2012b). This so-called post-

anoxic injury is due to a number of cellular reactions in plants that can produce free radicals, which can damage lipids, proteins and carbohydrates and can cause a plant to deteriorate and even lead to death as Blohkina et al., (2003) and Frye & Grosse, (1992) could show for e.g. *Arabis hirsute*, *Triticum aestivum* and *Zea mays*. Apart from that, the performance of a plant after flooding not only has to deteriorate, but can also improve, as plants are able to recover from flood damage. This was observed at *C. monogyna* in both flooding experiments (chapter 3 and 4). This species is also known to recover well after flooding reported in Frye & Grosse, 1992.

In comparison to the first flooding experiment (chapter 3), in the second flooding experiment, similar species-specific flooding tolerance patterns emerged three weeks after flooding (chapter 4). This seems surprising as the individuals were one year older compared to the previous flooding experiment (chapter 3). It is known that flooding tolerance increases with age, as individuals grow above flooding water level and are thus exposed to a lower relative flooding depth. In addition, older individuals are able to develop adaptation mechanisms more quickly (Siebel & Blom, 1998). However, it must be taken into account that, due to their longevity, shrubs and trees are still in their early establishment phase at 14 months of age. Blom (1999), reports that changes in flooding survival of *F. excelsior* and *Q. robur* did not increase with age during their juvenile years. Furthermore, it was striking that all studied species showed a lower injury level after nine months of recovery and were therefore able to recover better after flooding than in the previous flooding experiment (chapters 3 and 4). The two species *S. nigra* and *C. sanguinea* were the exception, which had suffered so badly after the nine-week flooding that they were unable to recover (chapter 4). Overall, increasing age has a positive effect on recovery and thus on long-term flooding tolerance. Wright et al. (2017) observed a better recovery after flooding with increased root aerenchyma content, which also might be a reason for the better recovery of the one-year older plants in the second compared to the first flooding experiment (chapter 3 and 4). Further, also the level of reserve carbohydrates remaining after flooding is assumed to influence plant recovery (Striker, 2012b). Hence, a successful recovery after flooding depends greatly on having a high content of reserve carbohydrates. As mentioned above, species that continue to grow during flooding would be classified as flood-tolerant, while those that temporarily suspend their growth would be classified as flooding-intolerant without including a recovery period. To summarize, a poor performance during flooding does not necessarily mean a poor flooding tolerance (Striker, 2012b). How long such a recovery period has to last seems to depend on the respective species and its developmental stage. It would be interesting to investigate this topic in more detail.

### *Flooding stress memory versus flooding stress recovery*

In the flooding experiment with the recurrent flooding, an already experienced flooding event in the previous year, regardless of its duration, did not result in an improved flooding tolerance of the studied saplings (chapter 4). This indicated that there is no immediate flooding stress memory for the investigated species. In general, after stress events, there seem to be two main strategies, either to form a stress memory or to recover from stress damage (Crisp et al., 2016). Both strategies have advantages and disadvantages. While a stress memory may enable a better and faster adaptation to a recurrent stress, the formation of a stress memory may also delay the recovery from flood damage under favorable environmental conditions (Crisp et al., 2016). The key role of this process seem to anchored in the RNA turnover, which can either facilitate recovery by clearing the stress-responsive transcriptome or by permitting memory formation by selectively stabilizing transcripts (Crisp et al., 2016). As mentioned above, most species recovered very well after flooding (chapter 4). This seems to be the better option, particularly regarding unpredictable environmental conditions (Zhou et al., 2020). In addition, the ability to form a stress memory in long-lived trees may rather occur later in life and probably not during the first two years of establishment when the individuals are generally most vulnerable. Zweifel et al. (2020), found a delayed drought stress response in terms of restricted growth in adult pine trees only after two to four years after drought. Also flood damage can negatively affect plants up to two to three years (Glenz et al., 2006). Therefore, it is probably too early to draw conclusion about flooding stress memory for the investigated species. Moreover, genetic studies could be helpful to draw more precise conclusion. So far, the molecular basis of stress memory in plants is still in its infancy and is mainly carried out on herbaceous plants such as *Arabidopsis thaliana* (Shahnejat-Bushehri et al., 2016). In trees, another potential of stress memory was determined by passing down flooding stress memories to offspring to increase their success. This was observed in a floodplain population of the tropical Amazonian tree *Himatanthus sucuuba* (Apocynaceae) that was more tolerant to flooding in terms of a higher survival, growth and germination rate than an upland population of the same species (Ferreira et al., 2007). Therefore, it would be interesting to conduct and analyse further seed experiments with trees from the active floodplain compared to those from the fossil floodplain.

### *The role of oxygen content in flooding water*

Although the oxygen shortage is reported to be the main problem during flooding (Mommer & Visser, 2005), additional oxygen supply to the floodwater by aeration did not affect plants

performance (chapter 3). It has to be taken into account that the studied plant individuals were only partially flooded, leading to anaerobic conditions only in the root system of the plants. Species that were able to form adventitious roots, hypertrophied lenticels or aerenchym tissue, could therefore ensure their oxygen uptake by these structures as they were under normal atmospheric conditions. Conversely, flooding-intolerant species might be unable to benefit also from high oxygen levels due to the lack of capacity for internal gas transport when flooded (Jackson & Armstrong, 1999). However, there were only minor differences in oxygen content between both oxygen treatments. This could be related to the fact that all basins were set up outside and were exposed to wind turbulences and rain. In addition, also freshwater was regularly refilled to compensate evaporation. This led to an increased oxygen content, even for the basins without aeration. Moreover, with increasing flooding duration, in all basins, the oxygen concentration probably also decreased irrespective of aeration, due to the decreasing oxygen solubility with increasing temperature during summer (Colmer et al., 2011). As a result of the capacity of cold water to hold more dissolved oxygen, cold water is less damaging than warm water (Glenz et al., 2006). The study of Van Eck et al. (2005) showed for *Rumex acetosa* that plant performance in terms of biomass loss decreased due to higher water temperature rather than due to low oxygen concentration ( $1 \text{ mg L}^{-1}$ ) in water. Therefore, the lowest measured oxygen content of the study in chapter 4 ( $3.1 \text{ mg L}^{-1}$ ) was probably not low enough to determine ecological impacts on plant development (chapter 3). For comparison, a critical oxygen content for fish in water is below  $3 \text{ mg L}^{-1}$  (Franklin, 2014). Further, flooding tolerance is not only influenced by the oxygen content of the water, but also by the concentrations of other chemical compounds, being able to interfere with biochemical pathways (Glenz et al., 2006). This chemical compounds can also influence the ability to control metabolism, the availability of abundant energy resources and, finally, the protection against post-anoxic injury (Armstrong et al., 1994; Glenz et al., 2006). Therefore, the plants' own adaptation mechanisms to flooding determine their flood tolerance to a far greater extent than just the oxygen content of the water.

#### *Hardwood floodplain forest species under natural field conditions*

In the field study, flooding duration means the annual number of flooding days per year and per vegetation period (chapter 2). The studied species (*U. laevis*, *Q. robur*, *C. monogyna*) were located along the relative elevational gradient and thus being expressed by a decreasing numbers of flooding days, according to their flooding tolerance (chapter 2). This means that *U. laevis* is located at the lowest sites where it has to tolerate the highest number of flooding days, followed by *Q. robur* and finally *C. monogyna*, probably being the result of their species-

specific mechanisms to adapt to flooding conditions as explained in the context of the two flooding experiments. Further, it was clearly shown that the trees planted in the course of the dike relocation were located at lower relative elevations compared to the individuals outside the dike relocation area within the surrounding active floodplain and therefore had to tolerate more flooding days. Furthermore, due to the complex morphology of the dike relocation area and its special flooding and flow dynamics, the conditions differ from the active floodplain in the surroundings (Faulhaber et al., 2013). For example, numerous flood channels, depressions and barriers alter the flow and sedimentation in the dike relocation area, resulting in a comparatively slow backflow into the Elbe (Krüger, 2012). This means that the already higher number of flooding days inside the dike relocation area, due to its lower elevation, additionally increases due to its complex morphology. Therefore, flooding duration cannot be derived from the relative elevation alone, as it is controlled also by many other additionally factors. For example, flooding duration is also influenced indirectly via soil and groundwater balance (Krüger, 2012). Since the dike relocation area consists mainly of well-permeable sands and gravel sands, the groundwater level often depends directly on the river (Montenegro, 2013). Groundwater fluctuations are greatest near the river and decrease with increasing distance (Pott, 2000). However, depending on the location, the formation of a small-scale micro-relief can occur, since the different stratification and thickness of the soil substrates (gravel, sand, clay, loam, silt) influence the water storage availability and, accordingly, the soil moisture ratio (Montenegro, 2013).

Although the mean number of flooding days inside the dike relocation area were within the typical growth range of hardwood floodplain forests, the survival rate of the trees planted from 2004 up to 2008 was very low during the success control in 2016, where 7% of the planted trees were recorded (Purps, 2016). Altogether, only 10% of *U. laevis*, 3% of *Q. robur* and 1% of *C. monogyna* survived (Purps 2016). This was probably caused by a series of flooding stress events already in the first years subsequent to the opening of the old dike. Besides the winter floods in 2011 and 2012, together with a massive ice cover that damaged the young trees mechanically, the summer flood of 2013 was certainly also a decisive factor for a high mortality. In general, due to higher metabolic activity, flooding during the growing season is much more harmful to plants than during winter season (Vreugdenhil et al., 2006). The study of Hall & Smith (1955), who studied the effects of flooding on woody plants, showed that even the most flooding-tolerant species (*Ulmus americana*, *U. alata*, *Populus deltoids*, *P. monilifera*) need to be unflooded for at least 55–60% of the growing season in order to survive. During the 2013 summer flood, the individuals were flooded over a time span up to 50% of the growing season

(chapter 2), which means that the duration of the unflooded period during the growing season was already exceeded. Further, several flood damage effects may still have an impact over two to three years (Coder, 1994; Glenz et al., 2006). Therefore, the required recovery time may exceed the time between two floods, resulting in an additional weakening of the trees as they are unable to recover from the previous flood (Dister, 1983; Glenz et al., 2006).

In contrast to the period from 2011 to 2013 with extreme flooding events, the following period from 2014 to 2017 was characterized by very dry years, leading to further stress for the young trees. Therefore, also this drought period can be considered as a three-year extreme event. One of the main effects of drought is an impaired germination and therefore a poor establishment of the plants (Farooq et al., 2009). Drought also negatively affect the growth and development of seedlings and is considered to be the main reason for seedling mortality (Evans & Etherington, 1991; Ludewig et al., 2018; Moles & Westoby, 2004). Particularly shortly after emergence, when seedlings switch from internal to external resource use, seedlings are most sensitive to a lack of moisture (Harper, 1965; Ludewig et al., 2018). Severely reduced germination and bad establishment of the studied hardwood floodplain forest species were also evident in another field experiment that I conducted in the same dike relocation area during the drought period from 2017 to 2020. Unfortunately, due to a low germination- and high mortality rate, the final data availability was very limited. Therefore, this study has not been published. Nevertheless, due to its scientific value and its practical relevance, it will be briefly described here. The aim of the study was to investigate the germination of seven different hardwood floodplain forest species (*A. pseudoplatanus*, *C. monogyna*, *C. sanguinea*, *F. excelsior*, *Q. robur*, *U. laevis*, *Viburnum opulus* L.) along the prevailing hydrological gradient in the dike relocation site. Therefore, the hydrological gradient was divided into three elevational stages (bottom, middle, top) with a height difference of 25 cm between each stage. Within each stage, five plots were set up, consisting of 14 sub-plots serving as sowing areas. In April 2017, 20 seeds of each shrub species (*C. monogyna*, *C. sanguinea*, *V. opulus*) and 10 seeds of each tree species (*A. pseudoplatanus*, *F. excelsior*, *Q. robur*, *U. laevis*) were sown, resulting in a total of 1,500 seeds. During the following four years (2017–2020), the number of emerged seedlings and the establishment phase in terms of growth (e.g. plant height, number of leaves) were recorded twice a year. Overall, only 7.7% of the seeds germinated, regardless of the position on the hydrological gradient. In the following years, further of the emerged and remaining saplings died. In 2020, only 5.8% survived on the lower, 5.1% on the middle and 3.6% on the upper plots. Of all species, *Q. robur* showed the highest germination and early establishment success with 52.6% whereas not a single seed of *U. laevis* germinated. The good germination and early

establishment of *Q. robur* may be due to its additional drought tolerance due to its pronounced taproot (Bonfils et al., 2013) as well as due to the nutrient advantage of its large seeds. For example, also Schnitzler (1997) showed *Q. robur*'s tolerance to a low water- and nutrient availability in its early establishment phase. Of *C. sanguinea*, *C. monogyna* and *V. opulus*, the most individuals survived at the lowest plots, where probably at least a bit soil water still could have been available compared to the middle and upper plots. The failure of *U. laevis* to germinate is probably due to the fact that this species is restricted to moist soils (Venturas et al., 2014).

Even though natural floodplains show a continuous alternation of flooding and drought, neither long periods of flooding nor long periods of drought are favorable at the establishment phase (Mosner et al., 2009). This stage is the most sensitive life stage during a plant's life and therefore most vulnerable towards stress events (Cavers & Harper, 1967; Marks & Prince, 1981). The chosen observation period for the two field experiments (chapter 2 and unpublished results) represents a rather unfavorable time frame with both types of long-term extreme events during the establishment phase. Therefore, the mean values of the annual flooding duration for the period from 2011 to 2017 should be considered with the background of the effects of flooding and drought periods, separately. Nevertheless, such time frames show how dynamic processes in floodplain forests are and that longer study periods are necessary to get a better understanding of the underlying processes. It can be assumed that under natural conditions almost no establishment and natural regeneration of hardwood floodplain forest species would have taken place inside the dike relocation area during the period under study (2011–2020; chapter 2 and unpublished results).

#### *Additional factors controlling germination and establishment under natural field conditions*

Besides the hydrological conditions, many other factors can influence the establishment of trees, which also became evident for the field studies (chapter 2 and study with unpublished results). For example, herbivory is a decisive factor in the study area. Thus, the few individuals that have been able to establish despite the extreme conditions were threatened by damage of a high wildlife density (Reif et al., 2016). Even if the already established woody plants do not die immediately due to browsing by wild boar, roe deer or rodents, the development is permanently slowed down. Thus, the affected trees cannot grow out of the danger zone of flood events and can die more quickly due to reduced vitality in the case of additional stress (Purps, 2016). In addition, also seed predation can be a limiting factor for germination. For example, the study



of Venturas et al. (2014), showed, that *U. laevis* is only able to regenerate in mast years, when conditions are optimal while in non-mast years, post-dispersal predation provide almost no chance for *U. laevis* to regenerate (Venturas et al., 2014). This could also be a reason why no seed of *U. laevis* germinated in the unpublished study described above. Therefore, mast years have a special relevance for regeneration due to the huge number of seeds escaping predation resulting in relatively high germination and establishment rates (Venturas et al., 2014). However, no mast year took place during the study period (2017–2020; unpublished results).

Another limiting factor for successful germination and establishment of hardwood floodplain forest tree species is the dense vegetation cover inside the dike relocation area, due to a high nutrient availability and favourable soil conditions (Purps, 2016). Since the investigated trees need open ground and high light availability during establishment, also this dense vegetation cover negatively affects tree establishment (Purps, 2016). Therefore, the natural tree establishment inside the dike relocation area seems to be principally constrained to higher sites where the effect of a lower nutrient content and thus a more open vegetation cover is more important than the low flooding duration (Pott, 2000; Purps, 2016). This is probably also the reason, why the individuals of the surrounding active floodplain established successfully at these higher lying areas under natural conditions (chapter 2). Although open ground is ensured in plantings, natural regeneration can still be hindered in the future as soon as it is overgrown again. Additionally, also more competitive, non-native species can benefit from the open grounds, such as *F. pennsylvanica* and *A. negundo*, which are also already present in the Middle Elbe River section. As I showed in the two experimental studies (chapter 3 and 4), these species cope well with nine weeks of flooding, even if occurred already during the early establishment phase. While monitoring the success of hardwood floodplain reforestation in the “Kliekener” floodplain, Glaeser et al. (2009) showed, that the natural establishment rate of *F. pennsylvanica* was higher than those of the plantings of *Q. robur*, and that regardless of the fact that only one single tree of *F. pennsylvanica* was available as seed source. Due to its high degree of presence and further spread as well as its high flooding tolerance (also shown in chapter 3 and 4), this species is already assessed as invasive on hardwood floodplain forest sites at the Middle Elbe River region (Schmiedel, 2010). Also *A. negundo* is regarded as highly flooding-tolerant, but this species prefers more open spaces with enough light availability and low competition (Kowarik, 2003). Probably therefore, due to the dense vegetation cover in the Middle Elbe River region, this species is not that wide spread in the area. These examples show that the competitive potential of non-native species should be taken into account in restoration areas, too.

### *Implications for restoration projects and perspectives for future research*

Due to the complexity of interacting processes in floodplains, the knowledge about flooding tolerance of many hardwood floodplain forest species is still quite sparse and, in some cases, contradictory. Regardless of the multitude of influencing factors on flooding tolerance, this is not surprising, since most studies did not include a recovery period after flooding when species are either able to recover from flood damage or suffer even more under post-anoxic injury (Armstrong et al., 1994; Glenz et al., 2006; Striker, 2012b). In both experimental studies, I could clarify the importance for the assessment of flooding tolerance to include also a recovery period in order to avoid misjudgements in flooding tolerance patterns. Nevertheless, further research is needed on the role of the recovery period and its influencing factors.

Since for the investigated species, the predominant strategy after flooding was to recover instead of forming a flooding stress memory, recurring floods without an adequately long recovery period could pose problems for the establishment of saplings in floodplains as the time between two flooding events may be too short for recovery. Such problems should also be taken into account for restoration planning processes, as the series of flooding stress events during the establishment was also one of the main reasons caused high mortality of the planted trees inside the dike relocation area (Purps, 2016). Nevertheless, also knowledge about flooding stress memory and stress recovery is still sparse and should be studied in more detail.

Due to the high flooding tolerance and the competitive regeneration potential of the two non-natives *A. negundo* and *F. pennsylvanica*, both species should be considered with caution in restoration areas. Once established, they effectively reduce the recruitment of native species saplings (Annighöfer et al., 2012; Hyatt, 2008). Consequently, knowing the requirements of non-native species during their early establishment phase can have important implications for the management in alluvial forest (Bobiec, 2012; Liira et al., 2011). Regarding hardwood floodplain forests, there is still need for further research and monitoring on the influence and effect of non-native species.

Although the assessment of flooding tolerance patterns for hardwood floodplain forest species under controlled common garden conditions are useful in restoration planning processes, they should be considered with caution and of limited transferability for restoration projects. This is because under controlled conditions, the variations in site conditions, hydrological parameters and ecological requirements that occur under natural conditions, are not taken into account. Therefore, it is important to combine controlled common garden experiments with field

experiments to also consider the interaction of the influencing factors and their interaction to obtain a more “realistic” picture of reality. The field studies in the dike relocation area have shown that the processes in floodplains are very dynamic and that a series of very wet and subsequently very dry years must be assessed as extreme events, which negatively affect hardwood floodplain forest establishment. However, the mean annual number of flooding days was within the typical growth range of the hardwood floodplain forest zone. Nevertheless, under natural conditions almost no germination and establishment of hardwood floodplain forest species would have taken place inside the dike relocation area during the period under study (2011–2020; chapter 2 and unpublished results). Although the randomly chosen observation period reflects rather unfavourable environmental conditions for the establishment of woody species, the results underline the importance of comparable multi-year studies in floodplains and, above all, longer study periods in general. Due to the sum of interacting processes, the simultaneous establishment and thus natural regeneration of a bigger number of hardwood floodplain forest species can be a very rare event. For example, it can occur only once in a while over decades, but if successful usually leading to the establishment of an entire cohort of trees. This results in a typical age structure where not all age classes are represented (Mosner et al., 2009; Reif & Gärtner, 2007). To conclude, the success of tree plantings depend largely on the hydrological situations in the year of the plantings as well as the subsequent years. Further, plantings are often costly and as it do not guarantee successful regeneration. Therefore, I would recommend not just relying on plantings but also allow natural succession, even if it takes a long time. So, the species that can cope with the current site characteristics would also establish in the long term. However, the dike relocation has been completed only ten years ago; therefore, there is still enough time for natural regeneration of hardwood floodplain forest species. Nevertheless, to gain a better understanding of the interacting processes in floodplains, the success of restoration measures should be closely monitored over longer periods and should also take the interaction of the various influencing factors into account. Only then, it will be possible to provide better predictions and possible solutions for future restoration measures.

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## **Chapter 2**

Three hardwood floodplain forest species experience different flooding durations inside and outside a dike relocation area at the Elbe River

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## Abstract

Floodplain forests became rare in Europe, due to anthropogenic changes. One important aspect in their restoration is to re-introduce flooding via dike relocation, as implemented at the Elbe River near Lenzen/Germany. How forest development is influenced by dike relocation is still unclear and difficult to predict. Inside the dike relocation area, most trees were planted. Due to high mortality, we asked if the relative elevation of the planted trees and thus number of flooding days inside the relocation area is comparable to the prevailing flooding regime in the surrounding active floodplain. Therefore, the positions of *Ulmus laevis*, *Quercus robur* and *Crataegus monogyna* individuals were recorded using a DGPS and merged with a digital terrain model. Subsequently, relative elevation and number of flooding days for the entire year and for the growing season (mean for the years 2011–2017) were calculated. The most flooding tolerant species *U. laevis* occurred at the lowest sites and tolerates the highest number of flooding days, followed by *Q. robur* and finally by the least flooding tolerant species *C. monogyna*. All three species occurred at lower sites inside the dike relocation area and were exposed to longer flooding durations compared to sites outside. This is due to the complex morphology of this area and its special flooding and flow dynamics, which differ from the conditions in the surrounding active floodplain. Although the mean flooding duration is within the growth range of hardwood floodplain forests (Querco-Ulmetum), the majority of individuals may not have established at the planted sites under natural conditions. Therefore, we would recommend not relying only on plantings but also allowing natural succession. Then, the species that can cope with the hydrological site characteristics would establish also in the long term.

## Introduction

Floodplain forests are characteristic, azonal vegetation communities along floodplains worldwide (Richardson et al., 2007). Due to the high variability between flooding and drought conditions as well as their small-scale heterogeneity, they belong to the most species-rich habitats in Central Europe (Koenzen, 2005). In past centuries, many floodplain forests were cleared for settlements and agriculture (Colditz, 1994). For flood protection and to expand the European navigable waterways, dikes were constructed often near the riverbank, leading to a disconnection between floodplains and rivers (Damm, 2013). Such anthropogenic interventions changed the hydrological regime, leading to large losses of floodplains and their typical



vegetation. According to the alluvial status report for Germany, only 1% of natural hardwood floodplain forests are left in active floodplains (Brunotte et al., 2009). Due to the high nature conservation value of regularly flooded floodplain forests and their small area today, their conservation and restoration is an essential goal of nature conservation in river landscapes (Finck et al., 2002).

Dike relocation or dike realignment is one of the most effective methods to restore hydrologically dynamic floodplains, i.e. re-exposing them to periodically flooding. Former land use in areas where dike relocation takes place, is usually dominated by arable fields or cultivated grassland and thus plant communities that have not been exposed to flooding for a long time. Consequently, secondary succession takes place after changing the hydrological regime. This means that other species communities, better adapted to the new conditions will gradually replace the existing ones.

One of the largest completed dike relocation sites in Germany, with the objective of restoring floodplain forests, is located at the Elbe River near the city of Lenzen. This nature conservation project was implemented between 2002 and 2011 (Damm, 2013). During this time, a 6.1 km long new dike was built, up to 1.3 km inland of the old dike. The old dike was not completely removed but opened by six breaches, which resulted in an area of 420 ha hydrologically reconnected floodplain (Damm, 2013). To initiate and speed up the development of floodplain forests, trees were also planted on 77 ha of grassland from 2004 to 2008.

Under natural conditions, the zonation of woody species in floodplains is mainly determined by the hydrological regime (Blom & Voeselek, 1996). Minor variations in flooding frequency and duration result in distinct differences in species composition (Kozłowski, 2002). Softwood floodplain forests (*Salicetum triandro-viminalis* and *Salicetum albae*), can be found at lower elevations with more frequent and prolonged flooding whereas hardwood floodplain forests (*Querco-Ulmetum*) are located at higher elevations, and are thus flooded less frequently and for shorter time (Siebel & Bouwma, 1998).

The main problem for terrestrial plants during flooding is the shortage of oxygen (Glenz et al., 2006), which can lead to reduced plant vitality or even death (Mommer & Visser, 2005). Therefore, species in floodplain forests must be adapted to changing water levels and flooding (Glenz et al., 2006). Flooding tolerance can be regarded as key factor for successful establishment and development of plants (Leyer, 2004; Glenz et al., 2006). However, not all plant species are equally vulnerable to flooding. For the investigated species, *U. laevis* is

considered to be the most flooding tolerant, followed by *Q. robur* and finally *C. monogyna* (Kozłowski, 1997; Schnull & Thomas, 2000; Glenz et al., 2006). Differences can be explained by the ability to react to resulting stress in morphological, physiological and metabolic terms (Glenz et al., 2006). Besides the two main decisive factors such as flooding frequency and duration, the seasonal timing influences plants performance, as flooding has little or no effect during the winter season, but can severely affect growth and survival of plants during the growing season due to a higher metabolic activity (Kozłowski, 1997; Siebel & Blom, 1998).

Due to the complex and unpredictable hydrodynamics in floodplains, the success of floodplain restoration projects is difficult to predict and, as in the case of the dike relocation area (DRA), has resulted in low survival of planted trees. Furthermore, it is known that the hydrodynamics inside the DRA after opening the old dike do not correspond to the natural conditions before the dike construction (Faulhaber et al., 2013), as the backflow of flooding water is comparatively slow (Krüger, 2012). To increase the success of future restoration projects, we want to assess whether the planted trees inside the DRA were exposed to longer flooding durations compared to the individuals occurring in the surrounding active floodplain. Consequently, we investigated the occurrence of three hardwood floodplain forest species (*Q. robur*, *U. laevis* and *C. monogyna*) inside and outside the DRA. It can be assumed that sites at higher relative elevation will be flooded for shorter periods and less often than sites at lower relative elevation, and that there are species-specific differences depending on flooding tolerance. Therefore, we tested the following hypotheses:

1. Due to their flooding tolerance, *U. laevis* will be able to occur at the lowest elevations and therefore exposed to the highest annual number of flooding days, followed by *Q. robur* and finally *C. monogyna*.
2. Species differ in their occurrence along the elevational gradient inside the DRA compared to the surrounding active floodplain and have to tolerate higher annual number of flooding days inside than those outside the DRA.

## Methods

### Study site characteristics

The study area lies in the floodplain of the German lower Middle Elbe River section, including the dike relocation area near Lenzen and 40 km up- and 20 km downstream along the main river channel (Fig. 2.1). This area belongs to the Biosphere Reserve Elbe River Landscape and is a site of pan-European importance according to the European Habitats Directive (MLUL & LfU, 2017). The discharge of the Elbe is characterized by spring floods with beginning of snow melting in the Czech Giant Mountains, while summer floods are rather rare (Leyer, 2002). Phases of low water discharge usually occur between July and October. The study region belongs to a transitional climate zone between the maritime climate of Western Europe and the continental climate of Eastern Europe. The average annual temperature is 9.7 °C and the mean annual precipitation was 607 mm for the years 1995–2017 (DWD, 2018).

The characteristic vegetation of the area is a mosaic of fallow grassland, floodplain meadows, forb communities and initial floodplain forests from man-made plantings. The forests consist mainly of the plant communities *Salicetum triandro-viminalis* and *Salicetum albae* and the *Querco-Ulmetum laevis*. The latter is dominated by *U. laevis*, *Fraxinus excelsior*, *Q. robur* in the tree layer as well as *C. monogyna* and *Cornus sanguinea* in the shrub layer.

### Study species

The three species, *Q. robur*, *U. laevis* and *C. monogyna* are native to temperate regions in Europe (Meusel et al., 1965; Caudullo & De Rigo, 2016). They are typical forest species of the hardwood floodplain (*Querco-Ulmetum*) and they are often distributed in wet lowlands and floodplains along rivers due to their tolerance to periodic flooding (Jäger et al., 2017). They prefer fertile and nutritious clay soils (Jäger et al., 2017). *U. laevis* is considered to be highly flooding tolerant, followed by *Q. robur*, while *C. monogyna* is classified as intermediate flooding tolerant (Glenz et al., 2006).

### Selection of transects

In the active floodplains of the DRA and within an area 40 km up- and 20 km downstream of the DRA, transects were defined using ArcGIS 10.5 (Fig. 2.1). For transect selection, information about the distribution of the target species was obtained from the administration

offices of the “Elbe-Brandenburg River Landscape Biosphere Reserve” and the “Lower Saxony Elbe Valley Biosphere Reserve”. This ensured that the respective species were present in each transect. Each transect was 100 m wide and ran at a 90° angle from the centre line of the Elbe River to the dike, covering the entire elevational gradient. Four transects with a total area of 41.24 ha were defined inside the DRA, whereas nine transects with a total area of 42.94 ha were defined in the active floodplain outside the DRA (Fig. 2.1). Since the distance between the Elbe and the dike is very variable, approximately the same area size was used instead of using the same number of transects for both locations.

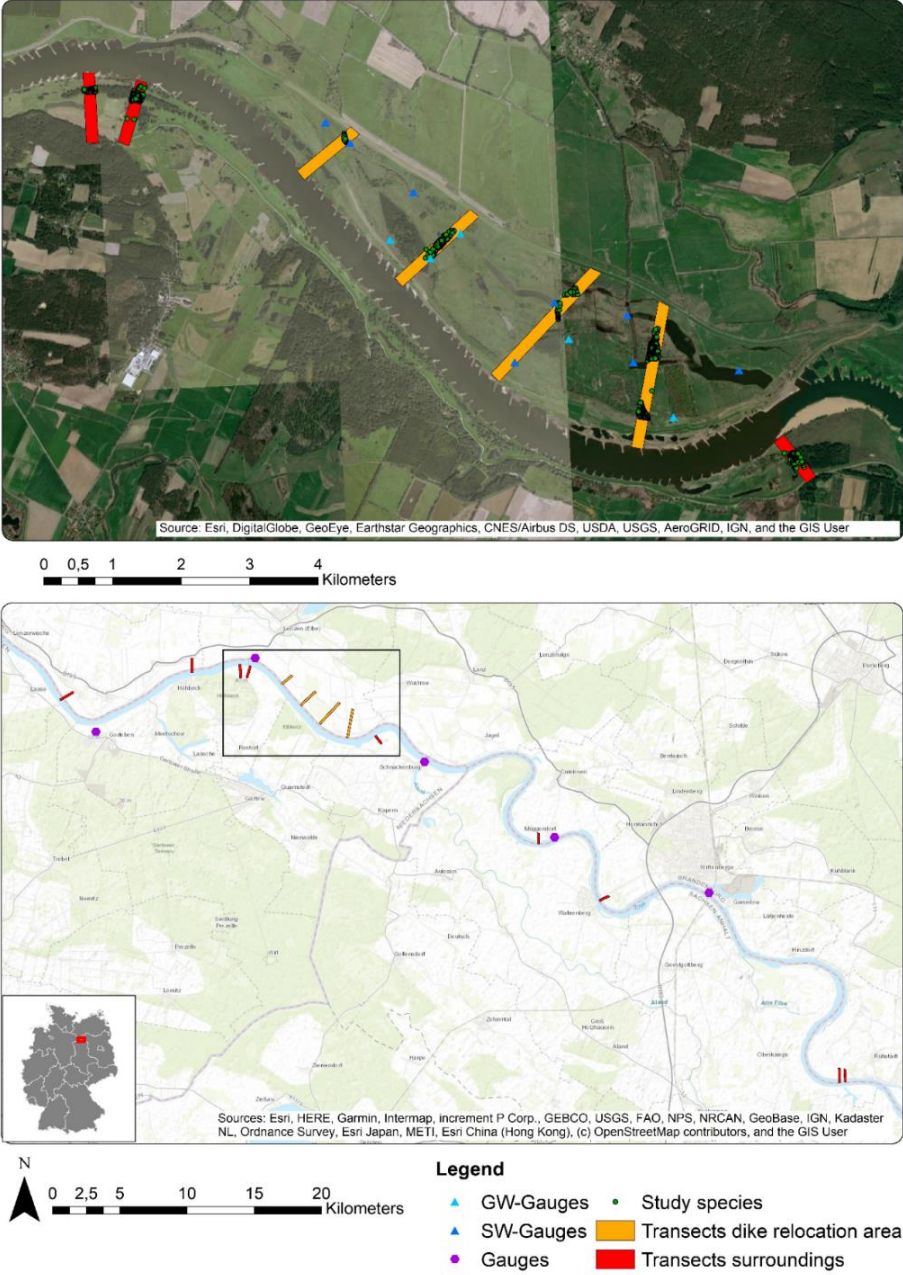


Fig. 2.1 Study area including transects, growth position of the study species in the DRA (orange) and its surroundings (red) and corresponding gauges.

## Data sampling

Data sampling in the DRA and the surrounding floodplain took place once per transect either from 7<sup>th</sup> to 25<sup>th</sup> of August 2017 or from 13<sup>th</sup> to 31<sup>st</sup> of August 2018. The position of all individuals of the study species of  $\geq 2$  m height (*U. laevis*, *Q. robur*, *C. monogyna*) was recorded precisely using a DGPS (Panasonic FZ-G1 Toughpad).

## Calculation of the relative elevation and number of flooding days

To calculate the Elbe water levels, the nearest corresponding river gauges in Sandau (Elbe km 416.10), Wittenberge (Elbe km 453.98), Müggendorf (Elbe km 463.94), Schnackenburg (Elbe km 474.56), Lenzen (Elbe km 484.70) and Gorleben (Elbe km 492.95) were used (Fig. 2.1). Based on these gauges, water level positions for the long-term mean runoff (MQ) for the entire study area were determined using stationary one-dimensional calculations (SOBEK), being available via the river hydrological software FLYS (BfG, 2013; reference period 1890–2006). As the morphology of the DRA is complex, 13 ground- and surface water measuring gauges (GW; SW) inside the DRA were used to increase the precision of the river gauges data (Fig. 2.1).

Based on the most up-to-date digital terrain model (DTM; grid size: 1 x 1 m; Brockmann et al., 2008), the relative elevation above mean water level of the Elbe of each individual growth position was calculated by subtracting the water level of the Elbe from the terrain height of the DTM.

Also based on the DTM, the number of flooding days (number of days with water levels above the elevation surface) for the entire year (January to December) and the growing season (1<sup>st</sup> of April to 30<sup>th</sup> of September) for the years 2011–2017 were calculated by interpolating each measured individual from the corresponding gauges. The interpolation was carried out using inverse distance weighting (Shepard, 1968). Since no additional gauge stations were available for the sites outside the DRA, there flooding duration was calculated based on the river gauges and the derived water level positions, respectively. In this case, no possible backwater effects in depressions or flood channels could be taken into account, so that the values there correspond to an idealised dynamic, i.e. unimpeded, inflow and outflow of water.

## Statistical Analysis

We analysed the relative elevation of the growing sites of the species and their number of flooding days for the entire year and growing season for the years 2011–2017 by conducting linear mixed-effect models (LMM). We used ‘*species*’ as fixed factor together with the parameters ‘*relative elevation*’, ‘*mean flooding days in 2011–2017*’ and ‘*mean flooding days during growing season 2011–2017*’ as response variables and included ‘*transect*’ as random factor for the mixed effect setup (Quinn & Keough, 2002).

To compare the relative elevation and number of flooding days, the individuals inside and outside the DRA were exposed to, separate LMMs were calculated. Therefore, we used the fixed factors ‘*species*’ and ‘*location*’ and their interaction and included the random factor ‘*transect*’. The parameters ‘*relative elevation*’, ‘*mean flooding days in 2011–2017*’ and ‘*mean flooding days during growing season 2011–2017*’ were used as response variables. Further, we analysed the years 2011–2013 separately to represent flooding conditions of normal (2012) and extreme years (2011 with extreme winter flooding; 2013 with extreme summer flooding).

For post-hoc testing, we used pairwise comparison with Tukey adjusted  $p$ -values. Mixed-effect models were carried out using the packages ‘lme4’ (Bates et al., 2015) and ‘lmerTest’ (Kuznetsova et al., 2017). We visually checked diagnostic residual plots to check the preconditions of the LMMs (e.g. normal distribution, variance homogeneity) (Zuur et al., 2010). The significance level for all analyses was  $\alpha = 0.05$ . All statistical analyses and figures were carried out using the R software environment (R version 4.0.3, 2020-10-10; R Development Core Team, 2020).

## Results

Altogether, 2,516 individuals were recorded in the transects (1,166 of *U. laevis*, 853 of *Q. robur* and 497 of *C. monogyna*). The relative elevation of the growing sites differed significantly between the investigated species ( $t = 21.84, 26.94, 10.44$ ,  $p$ -values  $\leq 0.001$ ), but also between the sites inside and outside the DRA ( $t = 4.82$ ,  $p$ -value  $\leq 0.001$ ). All occurrences of the species inside the DRA were at considerably lower relative elevations compared to those in the surrounding active floodplain (Fig. 2.2).

Inside the DRA, *C. monogyna* occurred at averaged 1.1 m above the Elbe mean water level, followed by *Q. robur* at averaged 0.66 m, while *U. laevis* grew at 0.57 m (Fig. 2.2). In the surrounding active floodplain, *C. monogyna* and *Q. robur* occurred 2.1 m above Elbe mean water level, while *U. laevis* grew at sites averaged 1.9 m (Fig. 2.2).

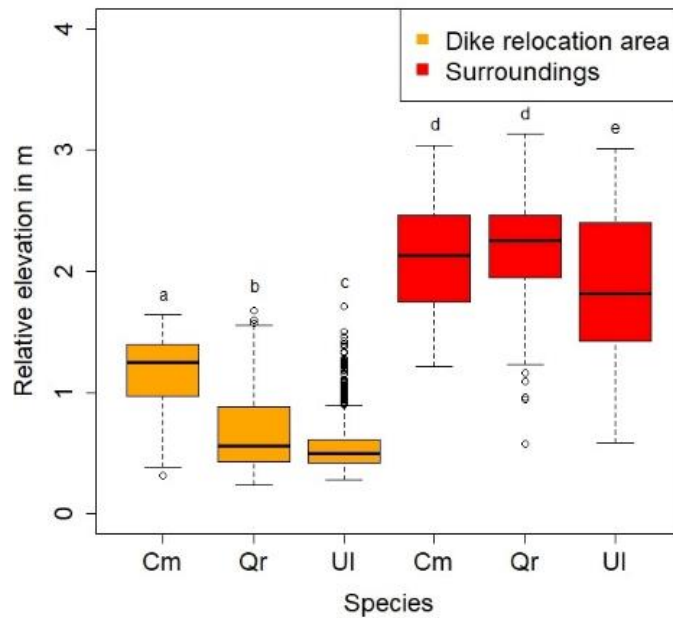


Fig. 2.2 Relative elevation in m above mean runoff (MQ) for each species inside the DRA (orange) and outside (surroundings; red) (Cm = *C. monogyna*, Qr = *Q. robur*, Ul = *U. laevis*; different letters indicate significant differences between groups assessed by Tukey Tests). The boxplot includes the box that represents the interquartile range (25<sup>th</sup> – 75<sup>th</sup> percentile), whiskers and median.

Inside the DRA, there were no differences in number of flooding days between *U. laevis* and *Q. robur*, but both showed a higher flooding duration compared to *C. monogyna*, for the entire year ( $t = 22.87, 28.64, p\text{-values} \leq 0.001$ ) and for the growing season ( $t = 19.75, 24.33, p\text{-values} \leq 0.001$ ; Fig. 2.3). In the surroundings, *U. laevis* was exposed to a higher annual flooding duration compared to *Q. robur* and *C. monogyna*, while there were no differences between the species during the growing season (Fig. 2.3). The range of flooding days within the species but also between the individuals of the same species, especially of *C. monogyna* was higher inside the DRA compared to those in the surroundings (Fig. 2.3).

The individuals growing inside the DRA were exposed to more flooding days compared to those in the surroundings for the period 2011–2017, namely 10–61 days throughout the entire

year and 5–24 days during the growing season. In contrast, those individuals in the surroundings had to tolerate 5–40 days throughout the entire year and 4–8 days during the growing season ( $t = 7.26, 6.66, p\text{-values} \leq 0.001$ ; Fig. 2.3).

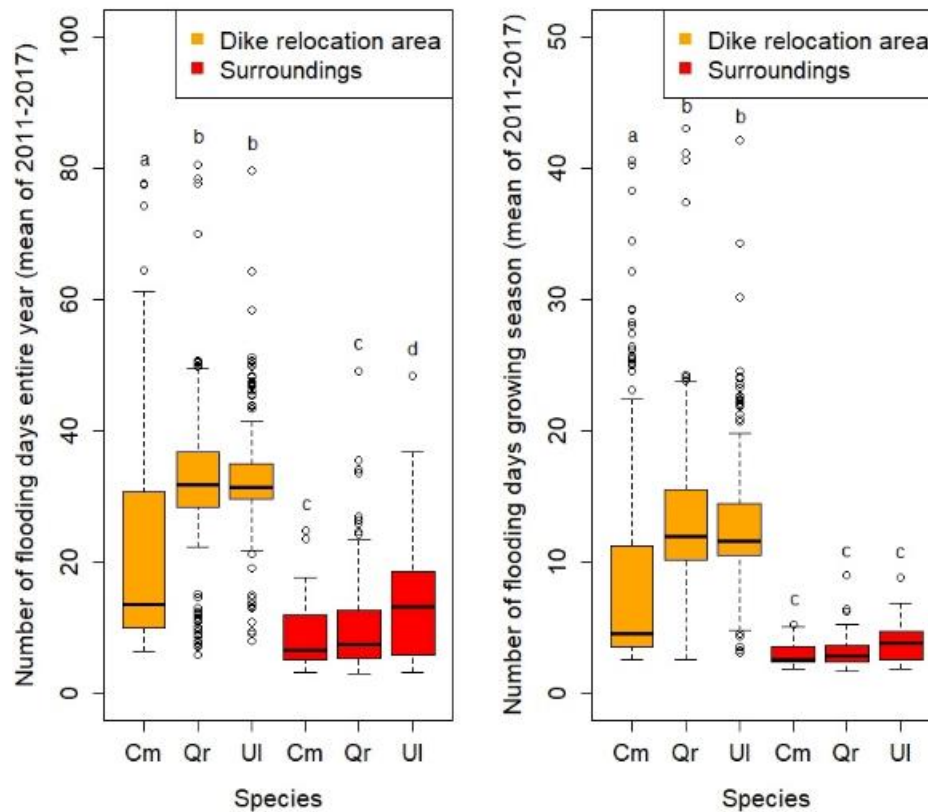


Fig. 2.3 Number of flooding days for each species for the entire year (left) (using mean values of the period 2011–2017) and during growing season (right) inside the DRA (orange) and for its surroundings (red) (Cm = *C. monogyna*, Qr = *Q. robur*, Ul = *U. laevis*; different letters indicate significant differences between groups assessed by Tukey Tests). Note different scaling of y-axes. The boxplot includes the box that represents the interquartile range (25<sup>th</sup> – 75<sup>th</sup> percentile), whiskers and median.

When considering the single years 2011, 2012 and 2013, *U. laevis* and *Q. robur* again showed a higher number of flooding days compared to *C. monogyna* inside the DRA, while *U. laevis* showed a higher flooding duration than *Q. robur* and *C. monogyna* in the surroundings ( $t = 28.09, 22.10, p\text{-values} \leq 0.001$ ; Tab. 2.1).

When focussing on the year 2011, flooding only occurred during the winter season for both locations. Regarding the entire year, there was an average of 44 flooding days for *C. monogyna* and 58 for *Q. robur* and *U. laevis* inside the DRA and about half as much for each species in



the surroundings (Tab. 2.1). In the “average“ year 2012, there were counted 24 flooding days for *C. monogyna*, 45 for *Q. robur* and 49 for *U. laevis* inside the DRA for the entire year, while there were 4, 6 or 11 outside the DRA, respectively. During the growing season, flooding occurred with averaged 18 flooding days for *Q. robur* and *U. laevis* only for the sites inside the DRA (Tab. 2.1). During 2013, a year with extreme summer flooding, *Q. robur* and *U. laevis* were exposed to an average of 106 flooding days throughout the entire year and 62 days during the vegetation period inside the DRA, in contrast to 34 or 45 and 23 or 26 days, respectively, in the surroundings (Tab. 2.1). *C. monogyna* was exposed to an average of 72 flooding days inside the entire year and 44 days for the growing season inside the dike relocation area, while the average number of flooding days for the surroundings were 29 for the entire year and 21 days during growing season (Tab. 2.1).

Tab. 2.1 Mean number of flooding days for each species for the entire year and during growing season in 2011, 2012 and 2013 inside the DRA (orange) and its surroundings (red) (Cm = *C. monogyna*, Qr = *Q. robur*, Ul = *U. laevis*).

Year/Species	Mean number of flooding days for entire year						Mean number of flooding days during growing season					
	Cm		Qr		Ul		Cm		Qr		Ul	
2011	44	25	58	29	58	34	2	0	2	0	0	0
2012	24	4	45	6	49	11	9	0	18	0	18	0
2013	72	29	106	34	106	45	44	21	62	23	62	26

## Discussion

The first hypothesis, that the occurrence of the species along the relative elevation gradient and thus the number of flooding days differs according to their flooding tolerance, can be confirmed. In general, *U. laevis* is located at the lowest sites and tolerates most flooding days, followed by *Q. robur* and finally *C. monogyna*. In general, a flooding duration typical for Querco-Ulmetum species to tolerate is 1 up to 85 days year<sup>-1</sup> (Pott, 2000). At sites along the Lower Middle Elbe, *C. monogyna* and *Q. robur* were flooded on average for five and 14 days but are able to endure

a maximum of 90 and 96 days per year, respectively, for the period from 1964 to 1998 (Pott, 2000). In comparison, *U. laevis* reached an average of 45 days but is able to survive at sites flooded up to 119 days per year (Pott, 2000). Our findings were within this range, however the averaged flooding days for *C. monogyna* as well as for *Q. robur* were higher than the averaged values of Pott (2000). While flooding adaptation of *C. monogyna* is poorly understood, *Q. robur* and *U. laevis* are known to have the ability to form aerenchym tissue, adventitious roots and lenticels to avoid a lack of oxygen at the roots (Glenz et al., 2006; Kramer et al., 2008; Heklau et al., 2019).

The second hypothesis, stating that the individuals inside the DRA were exposed to a higher number of flooding days compared to those outside, can be confirmed, too. Although the mean number of flooding days even inside the DRA were within the typical growth range of hardwood floodplain forests (Quercu-Ulmetum), the survival rate of the planted trees was very low during the control of success in 2016, where 7% of the planted trees were recorded (Purps, 2016). Altogether, only 10% of *U. laevis*, 3% of *Q. robur* and 1% of *C. monogyna* survived (Purps, 2016).

The reasons for the low survival rate of the planted trees was probably due to the successive stress events already directly in the first years after the old dike's opening. In addition to flooding during winter in 2011 and 2012, in 2013, an extreme flooding occurred during late summer (Purps 2016). The study of Hall & Smith (1955), who studied the effects of flooding on woody plants, showed that even the most flooding-tolerant species need to be unflooded for at least half a growing season in order to survive, which was exceeded during the summer flood 2013. As flooding is more harmful during the growing season, compared to the dormant season (Vreugdenhil et al., 2006), flooding duration should be reported not only for the entire year, but also for the vegetation period. Therefore, for future restoration measures, it is additionally important to consider also the flow regime of the respective river. For example, while the Elbe, as well as the rivers Main and Neckar are characterised by a nivo-pluvial discharge regime, where floods primarily occur in winter and rarely in summer, the Rhine River belongs to the nival discharge regime due to its alpine catchment area that is characterised by regular summer floods (Belz, 2010).

In general, the recorded species inside the DRA were located one to two metres above the Elbe mean water level, while the investigated area of the surroundings was about one metre higher. Since the investigated trees need open ground and high light availability during germination and establishment (Purps, 2016), a natural tree establishment in this area seems to be principally

constrained to higher sites, where the nutrient content is lower and thus a more open vegetation cover persists (Pott, 2000; Purps, 2016). Similar findings were observed in the study of Dister et al. 1992 on the River Rhine, where a successful immigration of hardwood floodplain forest species was only possible at higher, nutrient-poorer soils with a lower herb density. This is probably also a reason, why the individuals of the surrounding active floodplain established successfully at higher sites. The lower sites in this area were primarily dominated by floodplain meadows (Pott, 2000; Purps, 2016). Although open ground is ensured in plantings, establishment can still be hindered as soon as it is overgrown again.

While the first hurdle, namely germination, has already been successfully overcome in the case of plantings, under natural reproduction germination can be limited due to many factors. In addition to the species-specific environmental conditions and site characteristics that are needed for successful germination, seed predation can be a limited factor, too. For example, the study of Venturas et al. (2014), showed, that *U. laevis* is only able to regenerate in mast years, when conditions are optimal while in non-mast years, post-dispersal predation provide almost no chance for *U. laevis* to regenerate (Venturas et al., 2014). While the establishment of a single tree could be a very slow process, due to many influencing factors, and only occurs over a period of decades (Reif & Gärtner, 2007; Mosner et al., 2009).

Although the relative elevation of the individuals at both locations varied by about one metre, the number of flooding days inside the DRA fluctuated over a greater range than outside. This can be explained by the complex morphology of the terrain and its special flooding and flow dynamics that differ from the conditions of the active floodplain in the surroundings (Faulhaber et al. 2013). When the water level rises, the water first enters the area from downstream, which means against the flow direction of the Elbe main river channel, before it finally flows through the whole area from upstream at high water levels. This and the fact that the old dike is a considerable barrier, where the water can only exit at the six breaches, leads to a slow backflow into the Elbe (Krüger 2012). Therefore, the already higher number of flooding days, due to its lower elevation, additionally increases due to this reason. A slower backflow was also documented for the reconnected floodplain “Kühkopf-Knoblochsaue” at the Rhine River, where the dike broke in 1983 and was not fixed again (Dister et al. 1990). Further, for the study area at the Elbe River, it has to be kept in mind that the soil consists mainly of well-permeable sands and gravel sands, which leads to the fact that the groundwater level often depends directly on the river (Montenegro 2013). Therefore, flooding duration is also influenced via soil and groundwater balance (Krüger 2012). While the water sticks inside the DRA, it flows back

comparatively quickly in the surrounding floodplain. This illustrates how important also geomorphological processes are in addition to ecological and hydrological knowledge.

## Conclusion

In summary, the studied species occurred at different elevations according to their specific flooding tolerance and were generally exposed to a higher number of flooding days inside than outside the DRA. Although, the mean flooding duration is within the typical range of hardwood floodplain forests, the success of tree plantings depends largely on the hydrological situations in the year of the plantings as well as the subsequent years. As plantings are often costly and do not guarantee successful regeneration, we would recommend not relying exclusively on plantings, but also allowing natural succession, even if it takes a long time. Then, the species that can cope with the hydrological site characteristics would establish in the long term. To gain a better understanding of the interacting processes in floodplains, long-term monitoring programs should be carried out, ideally every five to ten years over ten to fifteen decades, as a hardwood floodplain forest requires a development period of around 100–150 years or longer (Bierhals et al., 2004; Scholz et al., 2012). Only then, it will be possible to provide better predictions and possible solutions for future restoration measures.

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## **Chapter 3**

### **Influence of flooding duration and aeration on saplings of ten hardwood floodplain forest species**

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## Abstract

Alluvial floodplain forests have been reduced drastically in many parts of Europe, due to deforestation, the transformation to settlement and expansion of agricultural areas. Although they have been heavily modified for centuries, generalized frameworks for their management are scarce and the complex interactions between the physical environment and biological processes are often not fully understood. As the zonation of woody species in floodplains is mainly determined by hydrological conditions, flooding tolerance can be regarded as a key factor for the successful establishment of woody species. Furthermore, the oxygen level of the flooding water might affect the responses to flooding. We examined the influence of flooding duration in combination with oxygen supply by aeration on the foliar injury and growth of six-week-old saplings of ten woody species, under controlled common garden conditions. Six of them are considered to be flooding tolerant whereas four are intolerant. In addition, seven are native whereas three are non-native species. During the experiment, the saplings were exposed to partial flooding of different durations ( $k = 3$ ; three, six and nine weeks) and oxygen levels ( $k = 2$ ; aerated and not aerated). For comparison, we included an unflooded control. We recorded foliar injury, plant height, number of leaves and stem diameter. We also included a recovery period of nine months. Whereas foliar injury decreased for most species with increasing flooding duration, the typical floodplain forest species, classified as flooding tolerant developed better. The differences in species response to flooding could be most likely explained by their ability to react to the resulting stress in morphological, physiological and metabolic terms irrespective whether they are native or not. In addition, the inclusion of a recovery period seems to be important for the assessment of flooding tolerance.

## Introduction

Riparian zones are the interface between aquatic and terrestrial ecosystems (Richardson et al., 2007). Due to their small-scale heterogeneity, they are hot spots of species richness and belong to the ecosystems with the highest biodiversity on earth (Naiman et al., 1993; Tockner & Stanford, 2002). However, due to deforestation, transformation to settlement and expansion of agricultural areas, alluvial floodplain forests have been drastically reduced in Germany and also in many other parts of Europe (Brunotte et al., 2009). The hydrological regime of the majority of floodplains have been dramatically changed because of the highly regulated rivers. The

floodplains getting more and more disconnected by dikes resulting in strongly altered flooding frequency and flooding duration (Brunotte et al., 2009). The remaining forests are highly fragmented, with the need for afforestation to re-connect fragments and increase connectivity. Although they have been heavily modified for centuries (Décamps et al., 1988; Washitani, 2001), generalized frameworks for their management are scarce (Holmes et al., 2005; Webb & Erskine, 2003; Wissmar & Beschta, 1998). In addition, the altered dynamics of riparian ecosystems can trigger the establishment and spread of non-native tree species in floodplains (Cooper et al., 2003; Cowie & Werner, 1993; Décamps et al., 1995; Hood & Naiman, 2000; Tickner et al., 2001; Washitani, 2001; Wissmar & Beschta, 1998). On top of this, climate change induced impacts on the alluvial plant communities add to the uncertainty about adequate conservation and restoration measures (Gattringer et al., 2019; Mosner et al., 2015). Whilst the recovery of floodplain forests is one of the most important objectives in alluvial restoration and for the conservation of biodiversity (Brunotte et al., 2009), the complex interactions between the physical environment and biological processes are not fully understood, which complicates restoration efforts (Rood et al., 2003).

Under natural conditions, the zonation of woody species in floodplains is mainly determined by the hydrological regime (Blom & Voesenek, 1996). In these systems, even minor variations in frequency and duration of flooding result in distinct differences in species composition (Kozłowski, 2002). Generally, there are two main floodplain forest types which can be distinguished (Blom & Voesenek, 1996; Hügin & Henrichfreise, 1992; Schnitzler, 1995): softwood floodplain forests are found at sites with more frequent and prolonged flooding and hardwood floodplain forests are found at sites flooded less frequently and for shorter time (Siebel & Bouwma, 1998).

A characteristic consequence of flooding is the temporary or permanent water saturation of soil pores, which causes substantial stress to terrestrial plants (Alaoui-Sossé et al., 2005). Thus, the species that grow in such habitats must be adapted to the changing water levels and flooding (Leyer, 2004; Mountford & Chapman, 1993). Flooding tolerance is therefore a key factor for the successful colonization of floodplain forests by plant species (Glenz et al., 2006; Streng et al., 1989). Particularly, the duration of flooding appears to strongly determine the survival of plants (Blom & Voesenek, 1996; Toner & Keddy, 1997). Generally, the longer trees are exposed to flooding the greater the damage is (Glenz et al., 2006). The main problem during flooding is the shortage of oxygen due to the slow diffusion rates of gases in water (Glenz et al., 2006). Thus, a reduction in oxygen availability results in a decreased photosynthesis (Glenz

et al., 2006), which in turn leads to a decline in growth rate, loss of biomass and eventually the death of the flooded plants (Mommer & Visser, 2005). However, not all species are equally vulnerable to flooding (Bockelmann et al., 2002; Lenssen et al., 1999; Silvertown et al., 1999; Sýkora et al., 1988). Therefore, flooding tolerant shrub and tree species have developed several adaptations to tolerate or avoid the effects of flooding (Vreugdenhil et al., 2006). Most of the adaptations to flooding are morphological adaptations (Glenz et al., 2006), such as hypertrophied lenticels, aerenchyma tissues and adventitious roots, which increase the uptake of oxygen by aerial tissues and promote oxygen transportation into the root system (Du et al., 2012). However, knowledge about the flooding tolerance of most Central European tree and shrub species is still incomplete (Glenz et al., 2006). In addition, conclusions on flooding tolerance have been mostly based on the responses during or immediately after the stress period, although it is the sum of plant behaviour both during and after the stress. Having survived flooding, poses new stress factors for plants during recovery (Striker, 2012). Therefore, plant recovery after flooding has often been overlooked but seems to be very important to avoid misjudgements (Striker, 2012).

The success of trees in flooded areas also depends on their age. Plants are most vulnerable during the sapling phase (Cavers & Harper, 1967; Marks & Prince, 1981). In contrast, adult trees are less sensitive to flooding than saplings of the same species (Gill, 1970; Hall & Smith, 1955; Kozłowski, 1997; Siebel & Blom, 1998). Thus, even the species rated as tolerant to flooding in later phases may be quite sensitive during the sapling stage (Glenz et al., 2006).

Besides the stressful physical environment, another threat to the regeneration of the native plant communities in the hardwood floodplain forests is the invasion by non-native tree species due to altered hydrological dynamics (Terwei et al., 2013). Kawaletz et al. (2013), for example, showed that once established, non-native trees effectively reduce the recruitment of native species saplings (Annighöfer et al., 2012; Hyatt, 2008). Consequently, knowing the requirements of non-native species during their early establishment phase can have important implications for the management of the non-native species in alluvial forest (Bobiec, 2012; Liira et al., 2011).

In summary, the success of restoration projects is based on the knowledge of the ecological, hydrological and geomorphological processes, as well as the flooding tolerance of the characteristic species based on the assessment after a certain recovery period (Glenz et al., 2006). While most of the studies on the flooding tolerance of trees have focussed on softwood

species, only a limited number of studies included hardwood forest species (Siebel, 1998; Van Splunder, 1998), even though they are usually much more threatened by human activities (Hartung, 2002). Consequently, to reduce this gap in knowledge, the effects of flooding on the survival and development of hardwood forest species needs to be investigated in more detail.

Therefore, we investigated the tolerance of six-week-old saplings of ten woody species to flooding in a controlled pot experiment. We included trees and shrubs, flooding tolerant and flooding intolerant species as well as natives and non-natives. In detail, we examined the influence of flooding duration in combination with oxygen supply by aeration on the foliar injury and growth of the saplings under controlled common garden conditions. As response variables, we assessed plant growth in terms of plant height, number of leaves and stem diameter as secondary growth. Specifically, we tested the following hypotheses:

1. With increasing flooding duration, the foliar injury and growth of the investigated woody species will be negatively affected, showing reduced plant height, less leaves and a reduced secondary growth. These negative flooding effects will be more pronounced for the intolerant species compared to the flooding tolerant species irrespective whether they are natives or non-natives.
2. The decrease in foliar injury and growth will be less pronounced with the addition of oxygen by aeration to the flooding basins.

## Methods

### Study species

We used woody species that show different degrees of flooding tolerance (Tab. 3.1). As representatives for flooding tolerant hardwood floodplain forest species of northern Central Europe, we selected *Q. robur* L., *F. excelsior* L., *C. sanguinea* L. and *C. monogyna* JACQ. We also included flooding intolerant species of northern Central Europe such as *Acer pseudoplatanus* L., *Sambucus nigra* L. and *Sorbus aucuparia* L., which already occur more often at higher altitudes of hardwood floodplains because of the increasing drought. In addition, we used three tree genera: *Acer*, *Fraxinus* and *Quercus*. For each of the three genera we tested a native and a non-native species (Tab. 3.1). The non-native species were *Acer negundo* L.,

*Fraxinus pennsylvanica* MARSHALL and *Quercus rubra* L. The reason to include non-native species were that in floodplains already non-native species such as *A. negundo* and *F. pennsylvanica* occur. In order to test the hazard potential of another non-native, but flooding intolerant species, we chose *Q. rubra* L. From the total of the above-mentioned species, six were classified as flooding tolerant and four as flooding intolerant (Tab. 3.1). We chose a rough classification to differentiate only between flooding tolerant and flooding intolerant species. The nomenclature of plant species follows Rothmaler et al. (2017).

Tab. 3.1 Information about study species, their family, origin and whether they are considered to be flooding tolerant in the literature (including citations).

Species	Family	Origin	Flooding tolerance
<i>Acer negundo</i>	Sapindaceae	North America, alluvial forests (Starfinger et al., 2011)	yes (Brink, 1954; Starfinger et al., 2011)
<i>Acer pseudoplatanus</i>	Sapindaceae	native	no (Frye & Grosse, 1992; Siebel, 1998)
<i>Cornus sanguinea</i>	Cornaceae	native	yes (Glenz, 2005)
<i>Crataegus monogyna</i>	Rosaceae	native	yes (Siebel, 1998; Vreugdenhil et al., 2006)
<i>Fraxinus excelsior</i>	Oleaceae	native	yes (Billetteft et al., 2002; Glenz, 2005)
<i>Fraxinus pennsylvanica</i>	Oleaceae	North America lowlands (Schmiedel & Schmidt, 2010)	yes (Schmiedel & Schmidt, 2010; Tang & Kozłowski, 1984)
<i>Quercus robur</i>	Fagaceae	native	yes (Billetteft et al., 2002; Colditz, 1994)
<i>Quercus rubra</i>	Fagaceae	Eastern North America (Starfinger et al., 2011a)	no (Colin-Belgrand et al., 1991)
<i>Sambucus nigra</i>	Adoxaceae	native	no (Glenz, 2005; Hoag & Landis, 2001; Westhus, 1986)
<i>Sorbus aucuparia</i>	Rosaceae	native	no (Brink, 1954; Frye & Grosse, 1992)

## Experimental setup

In a pot experiment, we investigated the influence of the flooding duration, in combination with or without oxygen supply by aeration with an aquarium pump, on the growth of the studied saplings. Three factor levels of flooding durations ( $k = 3$ ) were tested: short (three weeks), medium (six weeks) and long (nine weeks). In addition, we applied two oxygen treatments per flooding duration ( $k = 2$ ), which means that per flooding duration treatment the water in one basin was aerated with  $9 \text{ l} \cdot \text{min}^{-1}$  of air using an aquarium pump (Model AIR-8000) while the other was not. In addition, we had a control group without flooding and oxygen supply. In total, seven treatments were performed. For each species, seven replicates per treatment were conducted. With the ten above-mentioned species, this resulted in a total number of 490 plant individuals.

Seed collection took place along the Middle Elbe River in mid-September 2016 for the species *C. sanguinea*, *C. monogyna*, *S. nigra* and *S. aucuparia* and in early October 2016 for the other species (in a range of NW  $53^{\circ} 21' \text{ N}$ ,  $10^{\circ} 42' \text{ E}$  and SE  $52^{\circ} 58' \text{ N}$ ,  $11^{\circ} 38' \text{ E}$ ). The seeds were sampled from trees in the active and fossil floodplain along the Middle Elbe River. The collected seeds were kept cold and dry with sufficient air moisture until they were cold-wet stratified in potting soil in a climate chamber at  $4^{\circ}\text{C}$  following (Schubert, 1998) (Tab. A3.1). Subsequently, seeds were grown in a greenhouse during April and May 2017. At the end of May, all emerged seedlings were planted into pots (6 cm x 6 cm x 7.5 cm) filled with a 1:1 mixture of sand and commercial potting soil (Fruhstorfer Erde®, Type P, Industrie-Erdenwerke Archut GmbH, Lauterbach/Germany). The flooding experiment was set up at the research station Linden-Leihgestern of the Justus-Liebig University (Giessen, Germany,  $50^{\circ} 32' \text{ N}$ ,  $8^{\circ} 41' \text{ E}$ ) from June to September 2017. The seven basins consisted of a wooden frame of  $1 \text{ m}^2$  laid out with a 0.2 mm thick waterproof silage film (with the bright side upwards). The experiment was set up outdoors on a paved area exposed to ambient light, wind, temperature and precipitation. Each treatment group was randomly assigned to one of the seven basins while the pots with the saplings were randomly distributed within the basins. This setup resulted in a split-plot design because each treatment was located in one block (i.e. basin) to ensure manageability of the flooding/oxygen treatments. For the flooding treatment, all basins with the exception of the control basin, were filled with tap water up to 2 cm above the pot rim, i.e. plants were not completely covered by water. If necessary, evaporated water was refilled, so that water levels were kept constant during the flooding period. At the end of the flooding



treatment, the water was removed. Subsequently, those plants as well as the plants of the control were irrigated as required.

The experiment started on June 9<sup>th</sup> 2017. The oxygen content of the water was measured on a weekly basis. During the first two weeks, we used a JBL Testlab (JBL Testlab 25502, JBL, Neuhofen/Germany). Using this test set, the oxygen content was determined by a color change after the addition of two reagents. To increase the accuracy, we used an oximeter (WTW Oxi 325, Xylem Analytics Germany, Weilheim/Germany) to measure the oxygen content from the third week on. The oxygen content in the basins with aeration was significantly higher compared to the basins without aeration ( $p$ -value = 0.001; Fig. A3.1). In addition, the oxygen content decreased significantly from short to long flooding duration ( $p$ -value = 0.034; Fig. A3.1).

After the ninth week, when all individuals completed the flooding treatment, the plants were carefully repotted into larger pots (11 cm x 11 cm x 12 cm) to ensure optimal conditions. On September 1<sup>st</sup> 2017, which means twelve weeks after the start of the experiment, including a recovery period of at least three weeks for the longest flooding duration, foliar injury and growth of the individuals were recorded. The plant heights were measured as well as the stem diameter as secondary growth at the soil surface using a caliper. In addition, the number of leaves were counted. For the foliar injury of each plant, we defined five injury classes (1: all leaves without damage, 2: all leaves are fully developed but show damage < 50%, 3: leaves not fully developed and > 50% of them damaged, 4: all leaves damaged or dead, but plant is still alive, 5: plant dead). In June 2018, which means one year after the start of the experiment, including a recovery period of nine months, foliar injury was recorded again. During the whole time, the plants were watered when needed.

## Statistical analyses

For the comparison of the survival of the species between the flooded and control individuals and between the measurement after twelve weeks and after one year, we applied a two-way ANOVA. We used the factors '*species*', '*flooded individuals*' (flooded, control) and '*time*' (12 weeks, 1 year) as well as their interactions together with the parameter '*survival*' as the response variable. We visually checked diagnostic plots to test the preconditions of ANOVAs (e.g. normal distribution, variance homogeneity). For post-hoc testing, we used pairwise t-test with Holm adjusted  $p$ -values (Crawley, 2007).

We analyzed the effect of the treatments and control on the foliar injury of the saplings by conducting Scheirer-Ray-Hare-Tests (Puri & Sen, 1985). As response variables, the parameters ‘*foliar injury after twelve weeks*’ and ‘*foliar injury after one year*’ were used. We computed separate Scheirer-Ray-Hare-Tests for each species for both response variables with the factors ‘*flooding duration*’ (control, short, medium, long) and ‘*aeration*’ (control, yes, no) and their interaction (Crawley, 2007). For post-hoc testing, we used the Dunn Kruskal-Wallis multiple comparison with Benjamini-Hochberg adjusted *p*-values (Crawley, 2007).

To determine whether there were differences in foliar injury between the flooding tolerant and the flooding intolerant species, the Scheirer-Ray-Hare-Test was used with the same response variables (‘*foliar injury after 12 weeks*’ and ‘*foliar injury after 1 year*’). However, not all species were tested separately; rather the factor *flooding tolerance* (yes, no) was included to the factors. In order to investigate the comparison of natives and non-natives, only the three tree genera were used. Therefore, the factor ‘*native*’ (yes, no) was included to the factors. In addition, to compare the foliar injury after 12 weeks and 1 year, the factor ‘*time*’ (12 weeks, 1 year) was included to the factors and tested separately for each species.

In a next step, we tested the effects of the above-mentioned factors on the growth of the saplings. Therefore, we used the response variables ‘plant height’, ‘number of leaves’ and ‘stem diameter’ and computed separate split-plot-setup ANOVAs for each species. We excluded dead individuals from this analysis to avoid detrimental effects of zero values on ANOVAs. Before analysis, the variables were standardized using a natural logarithmic response ratio (RR) as suggested by Goldberg and Scheiner (Goldberg & Scheiner, 2001).

$$RR = \ln ( PT / \overline{PC} )$$

This standardization of the parameter value of the treated sample (PT) with the mean value of the control (  $\overline{PC}$  ) for each species allows species comparison. Effects of the treatments on the survived plants were considered significant (i.e. different from the controls) when 95% CI did not overlap with zero in Figures 3.4–3.6. Thereafter, ANOVAs for split plot designs were analysed for the factors flooding duration (short, medium, long), aeration (yes, no) and their interaction for every species and response variable (‘RR plant height’, ‘RR number of leaves’ and ‘RR stem diameter’) separately. For the post-hoc pairwise t-tests Holm adjusted *p*-values were applied (Crawley, 2007).

To determine differences of the growth between the flooding tolerant and the flooding intolerant species, the response variables ('RR plant height', 'RR number of leaves' and 'RR stem diameter' as well as the factors ('flooding duration', 'aeration' and their interaction) were used. Here too, not all species were tested separately; rather the factor 'flooding tolerance' (yes, no) was included in the analyses as well as the factor 'native' (yes, no) in the analysis for differences between native and non-native species.

For the analysis of significant differences in the oxygen content between the basins, we computed a Wilcoxon Signed Rank test because the preconditions for an ANOVA were not fulfilled and the transformation did not result in the necessary assumptions for normal distribution. For post-hoc testing, we used Dunn's test with Holm adjusted  $p$ -values (Crawley, 2007).

The significance level of all analyses was set up at  $\alpha = 0.05$ . All statistical analyses were carried out using the R software environment (R Development Core Team, 2017).

## Results

### Survival

Twelve weeks after the experiment started, 82% of the flooded individuals and 100% of the control survived (Fig. 3.1). With an average survival rate of 92%, almost all individuals of the flooding tolerant species survived the flooding irrespective of the flooding duration and aeration – except for *C. sanguinea*, which showed a comparatively low survival rate of only 58%. The flooding intolerant species showed a survival rate of 66% (Fig. 3.1). Significantly more individuals of *C. sanguinea* ( $p$ -value = 0.030), *Q. rubra* ( $p$ -value = 0.048) and *S. aucuparia* ( $p$ -value  $\leq 0.001$ ) survived the unflooded control compared to the flooded treatments (Fig. 3.1). One year after the flooding experiment started and after the recovery period of nine months, a further 24% of the flooded individuals were dead (Fig. 3.1). In total, 73% of the flooding tolerant species survived the flooding treatments compared to 33% of the flooding intolerant species. In the control, only 81% of the individuals survived after one year (Fig. 3.1). Especially *Q. rubra* showed a low survival rate of only 29% in the control (Fig. 3.1). Significant differences in the survival rate between flooded and control individuals were only visible for the flooding intolerant species *A. pseudoplatanus* ( $p$ -value = 0.017) and *S. aucuparia*

( $p$ -value  $\leq 0.001$ ). The survival of the native and non-native species did not differ significantly in relation to the treatments.

In general, the survival rate differed significantly between the species ( $p$ -value  $\leq 0.001$ ) and the time of measurement ( $p$ -value  $\leq 0.001$ ). In the flooded treatments, a significant decrease in the survival rate after one year compared to the measurement after 12 weeks were found for *A. pseudoplatanus* ( $p$ -value = 0.036), *F. excelsior* ( $p$ -value = 0.001), *Q. robur* ( $p$ -value = 0.008), *Q. rubra* ( $p$ -value  $\leq 0.001$ ) and *S. nigra* ( $p$ -value  $\leq 0.001$ ; Fig. 3.1). For *A. negundo* ( $p$ -value = 0.847), *C. sanguinea* ( $p$ -value = 0.7) and *S. aucuparia* ( $p$ -value = 0.84), almost all individuals that were alive after 12 weeks survived (Fig. 3.1). *Q. rubra* ( $p$ -value = 0.003) is the only species where significantly less individuals even of the control survived one year after the experiment started compared to 12 weeks (Fig. 3.1).

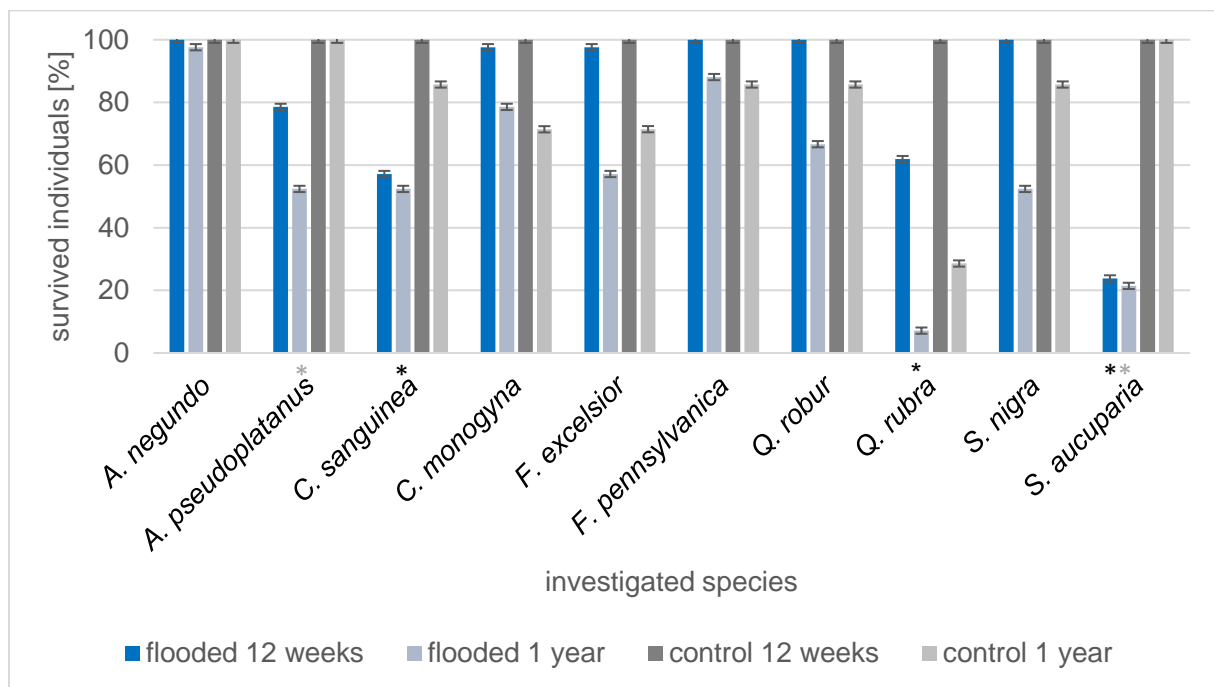


Fig. 3.1 Percentage of the survived individuals of each species in the flooded and control treatment twelve weeks and one year after the experiment started. \* indicates significant differences in the survival rate between flooded and unflooded control for that species after twelve weeks; \* after one year.

### Foliar injury

In general, with increasing flooding duration, the foliar injury of most species *A. pseudoplatanus* ( $p$ -value  $\leq 0.001$ ), *C. sanguinea* ( $p$ -value  $\leq 0.001$ ), *C. monogyna*

( $p$ -value = 0.001), *F. pennsylvanica* ( $p$ -value = 0.009) and *Q. rubra* ( $p$ -value = 0.003) increased twelve weeks after the start of the experiment (Fig. 3.2). Only *A. negundo*, *F. excelsior*, *Q. robur* and *S. nigra* showed an almost constant foliar injury over all flooding durations (Fig. 3.2). Significantly less foliar injury of the control compared to the medium and long flooding duration was visible for *A. pseudoplatanus* ( $p$ -values  $\leq 0.001$ ), *Q. rubra* ( $p$ -values = 0.002), *C. monogyna* ( $p$ -values  $\leq 0.001$ ), *C. sanguinea* ( $p$ -values  $\leq 0.001$ ), *F. excelsior* ( $p$ -values = 0.003, 0.001), *F. pennsylvanica* ( $p$ -values  $\leq 0.020$ , 0.001), and *S. aucupria* ( $p$ -values  $\leq 0.001$ ). The few surviving individuals of *S. aucuparia* showed a very high foliar injury (Fig. 3.2).

The aeration had no significant effect on foliar injury of the species. Whereas the flooding tolerant species showed a significantly lower foliar injury over all flooding treatments compared to the flooding intolerant species ( $p$ -value  $\leq 0.001$ ), the foliar injury of native and non-native species showed no significant difference ( $p$ -value = 0.096; Fig. 3.2).

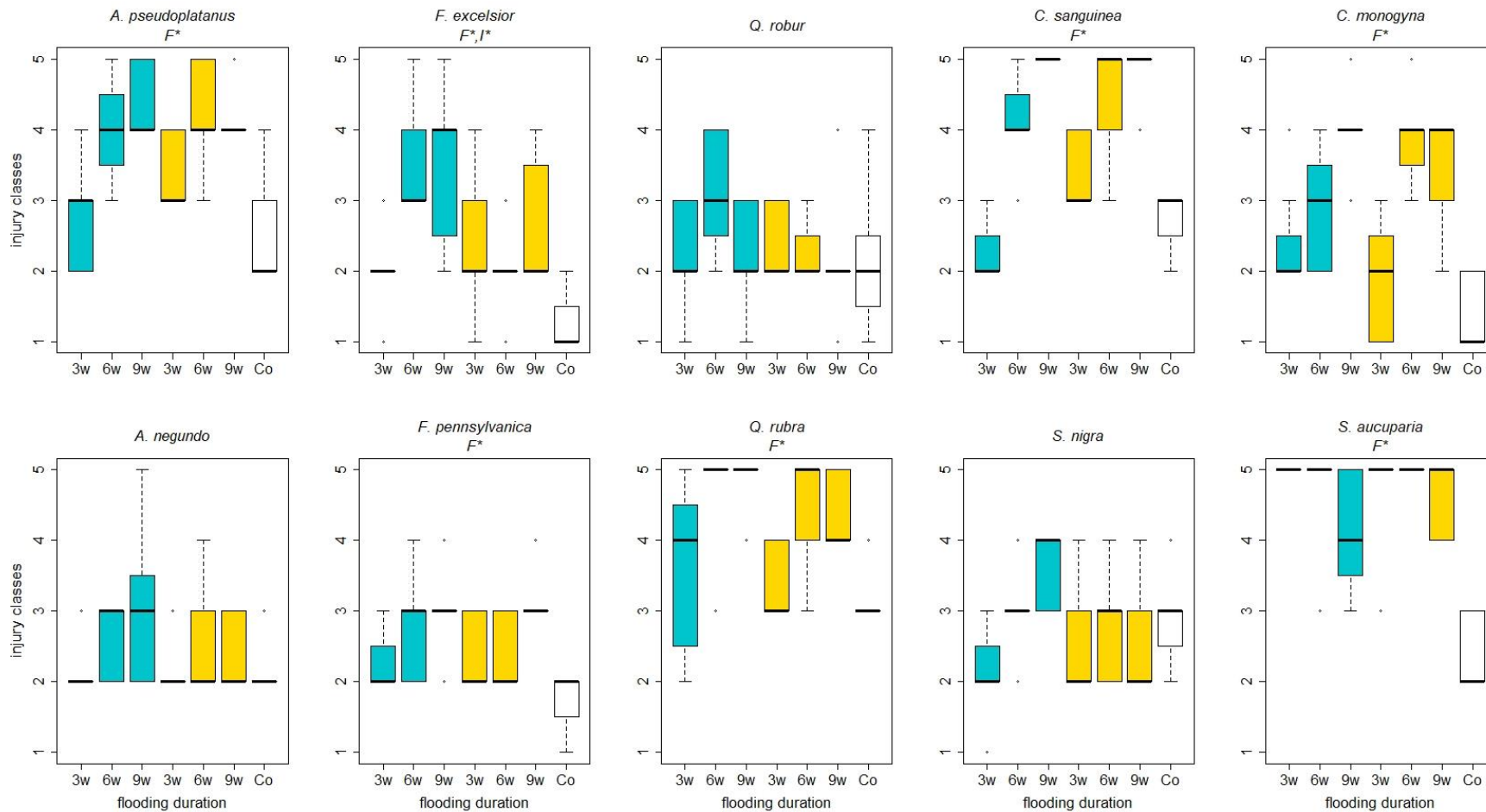


Fig. 3.2 Foliar injury of the species depending on the treatments 12 weeks after the experiment started. Injury classes from 1 (without damage) to 5 (dead); after 3 weeks (3w), 6 weeks (6w) and 9 weeks (9w) flooding duration and under control (Co) conditions without flooding and aeration.; Blue boxplots: oxygen supply by aeration, yellow boxplots: no aeration; significant differences between the main effects were marked with capital letters (F\* – Flooding duration, O\* – Oxygen treatment, I\* – Interaction between both).

One year after the start of the experiment, including a recovery period of nine months, the range of classification of the injury classes increased (Fig. 3.3). There was a significant increase in foliar injury from short to medium flooding duration for *A. pseudoplatanus* ( $p$ -values  $\leq 0.001$ ) and *C. sanguinea* ( $p$ -values = 0.042). *S. aucuparia* showed a significant increase in foliar injury from medium to long flooding duration ( $p$ -values = 0.036). The individuals of the control of *S. aucuparia* ( $p$ -values  $\leq 0.001$ ) and *S. nigra* ( $p$ -values = 0.03) showed a significantly lower foliar injury compared to the individuals of all flooding durations. The individuals of the control of *A. pseudoplatanus* ( $p$ -values = 0.003, 0.001) and *C. sanguinea* ( $p$ -values = 0.04, 0.001) showed a lower foliar injury compared to the medium and long flooding duration. For all species, the aeration showed no general pattern on the foliar injury (Fig. 3.3).

The flooding tolerant species showed again a significantly lower foliar injury compared to the flooding intolerant species ( $p$ -value  $\leq 0.001$ ). In addition, significant differences between the native and non-native species could be observed ( $p$ -value = 0.002). Whereas the two non-natives of the genus *Acer* and *Fraxinus* showed a significantly lower foliar injury compared to the natives, the reverse was true for the genus *Quercus*.

A comparison of the foliar injury after twelve weeks and after one year showed different results for the different species (Figs. 3.2 and 3.3). While the foliar injury of *A. negundo* ( $p$ -value = 0.008), *F. pennsylvanica* ( $p$ -value  $\leq 0.001$ ) and *C. sanguinea* ( $p$ -value = 0.03) decreased after one year, the foliar injury of *Q. robur* ( $p$ -value  $\leq 0.001$ ), *Q. rubra* ( $p$ -value  $\leq 0.001$ ) and *S. nigra* ( $p$ -value = 0.008) further increased (Figs. 3.2 and 3.3).

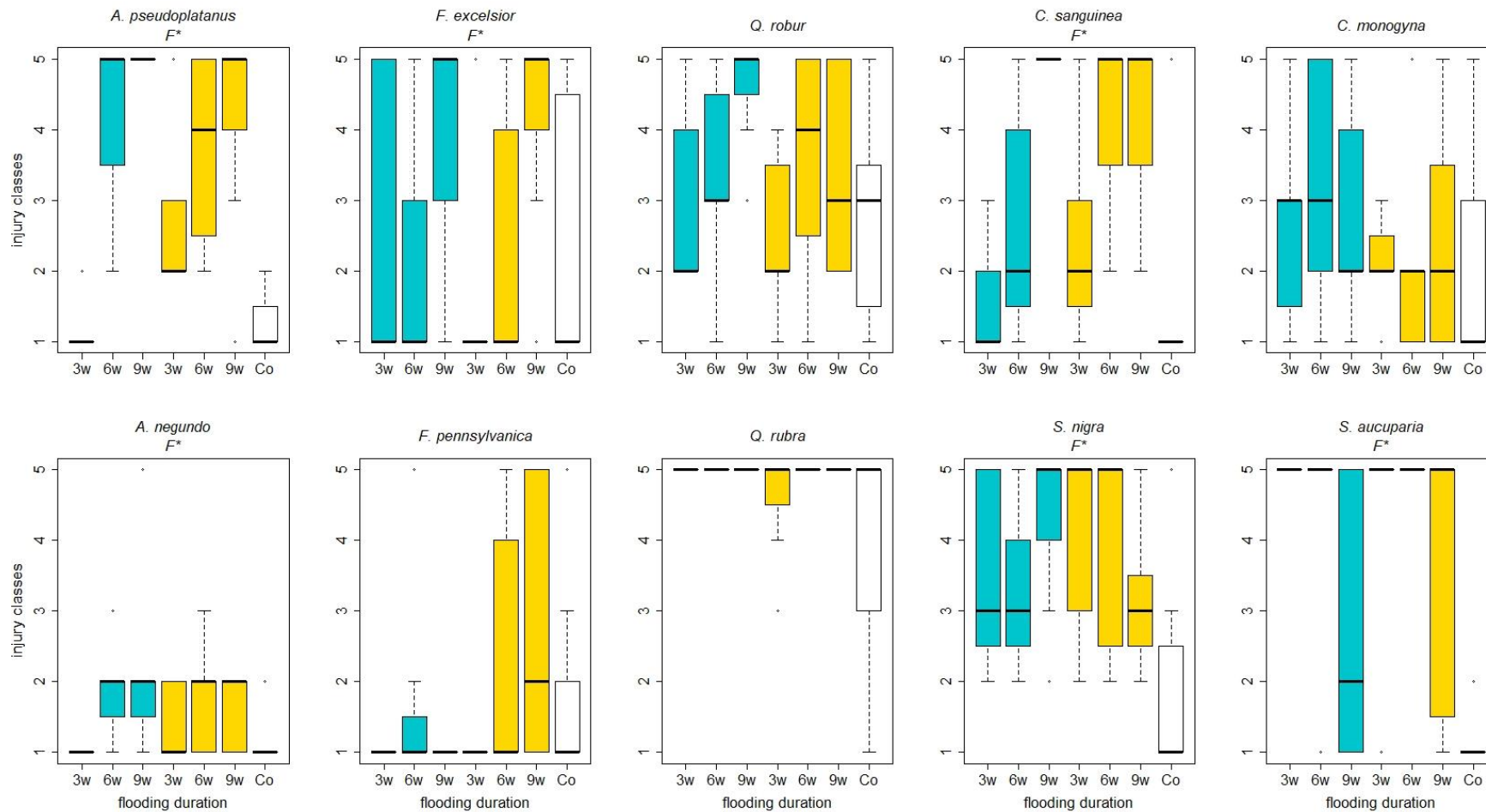


Fig. 3.3 Foliar injury of the species depending on the treatments one year after the start of the experiment, including a nine months recovery period. Injury classes from 1 (without damage) to 5 (dead); after 3 weeks (3w), 6 weeks (6w) and 9 weeks (9w) flooding duration and under control (Co) conditions without flooding and aeration.; Blue boxplots: oxygen supply by aeration, yellow boxplots: no aeration; significant differences between the main effects were marked with capital letters (F\* – Flooding duration, O\* – Oxygen treatment, I\* – Interaction between both).



## Plant height

Negative flooding effects on plant height for nearly every treatment compared to the control were significant for *A. negundo*, *C. sanguinea*, *F. pennsylvanica* and *S. nigra* (Fig. 3.4). For *A. pseudoplatanus*, *F. excelsior*, *C. monogyna* and *Q. rubra*, none of the treatments showed a significant difference in plant height from the control (Fig. 3.4). With increasing flooding duration, the height of *C. sanguinea* ( $p$ -value = 0.03) showed a significantly negative effect, while the significant differences in plant height between the short and medium ( $p$ -value = 0.002) and between the medium and long flooding duration ( $p$ -value  $\leq$  0.001) for *A. negundo* showed a less negative effect with increasing flooding duration. Without aeration there was a significantly more negative effect on the plant height of *F. pennsylvanica* compared to the individuals with aeration ( $p$ -value = 0.002; Fig. 3.4).

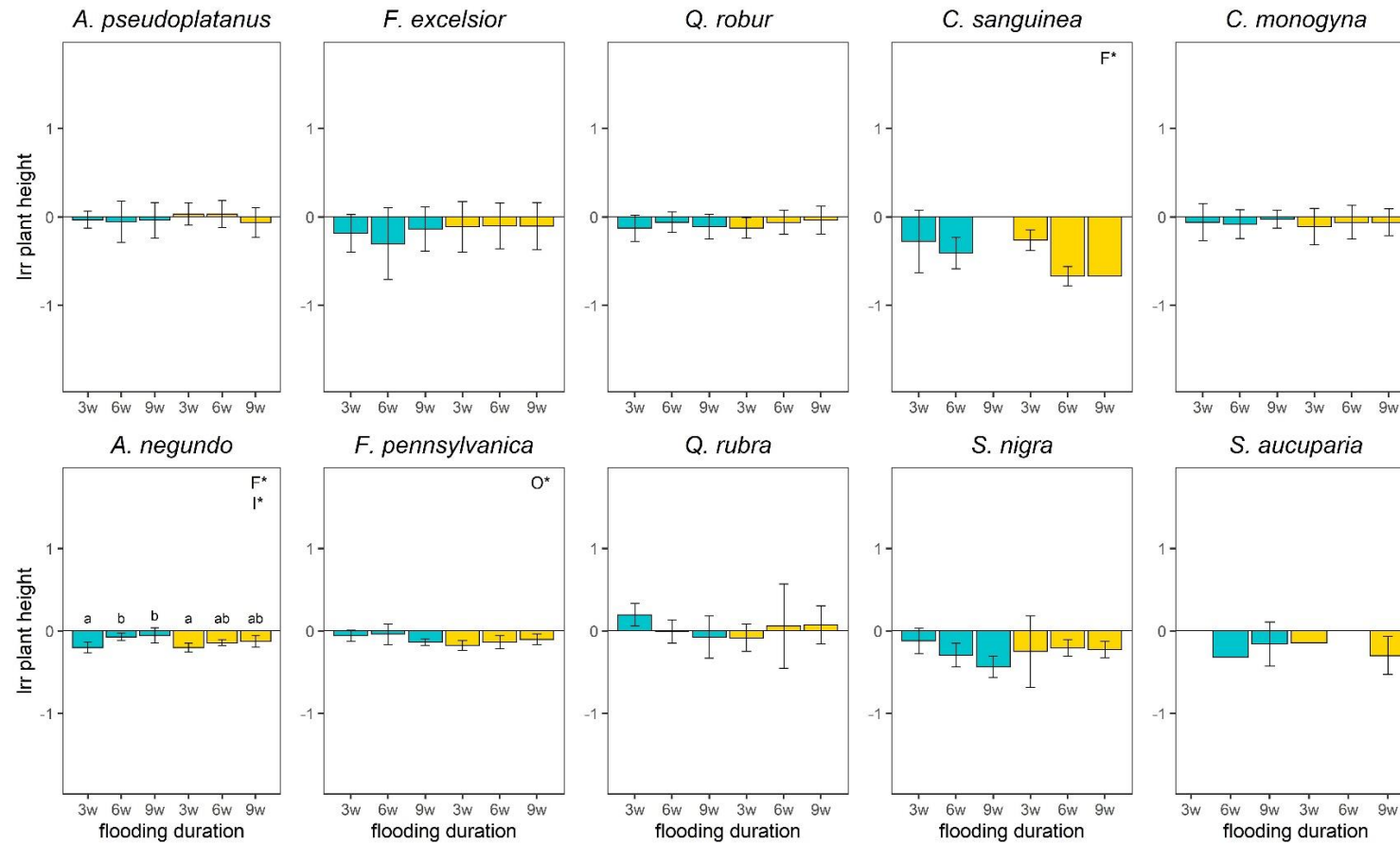


Fig. 3.4 Logarithmic response ratio (Irr) of plant height of the species depending on the treatments 12 weeks after the experiment started. w = weeks, the number prefixed indicates the flooding duration in weeks; Blue boxplots: aeration, yellow boxplots: no aeration; significant differences between the main effects were marked with capital letters in the upper right corner (F\* – Flooding duration, O\* – Oxygen treatment, I\* – Interaction between both); Effects of treatments on survived plants were considered significant (i.e different from the control) when 95% CI did not overlap with zero. Missing bars represent groups with a mortality of 100%. Missing CI represent groups with only one survival individual.

## Number of leaves

The number of leaves of *S. aucuparia*, *C. monogyna* and *A. pseudoplatanus* decreased at the long flooding duration irrespective of aeration or not. The combination of long flooding duration with aeration showed also a significantly negative effect compared to the control for *A. negundo* and *S. nigra* (Fig. 3.5). An increasing flooding duration from short to long showed a significantly negative effect on the number of leaves of *A. pseudoplatanus* ( $p$ -value  $\leq 0.001$ ), *A. negundo* ( $p$ -value = 0.04), *C. monogyna* ( $p$ -value  $\leq 0.001$ ) and *F. pennsylvanica* ( $p$ -value = 0.003). For *A. pseudoplatanus* ( $p$ -value = 0.03) and *C. monogyna* ( $p$ -value = 0.003), the number of leaves decreased also from medium to long flooding duration and for *C. sanguinea* ( $p$ -value = 0.001) from short to medium flooding duration. No significant difference in the number of leaves compared to the control were visible for *F. excelsior*, *F. pennsylvanica*, *Q. robur* and *C. sanguinea*. The oxygen treatment showed only a significantly negative effect on the number of leaves for *F. excelsior* with aeration (Fig. 3.5).

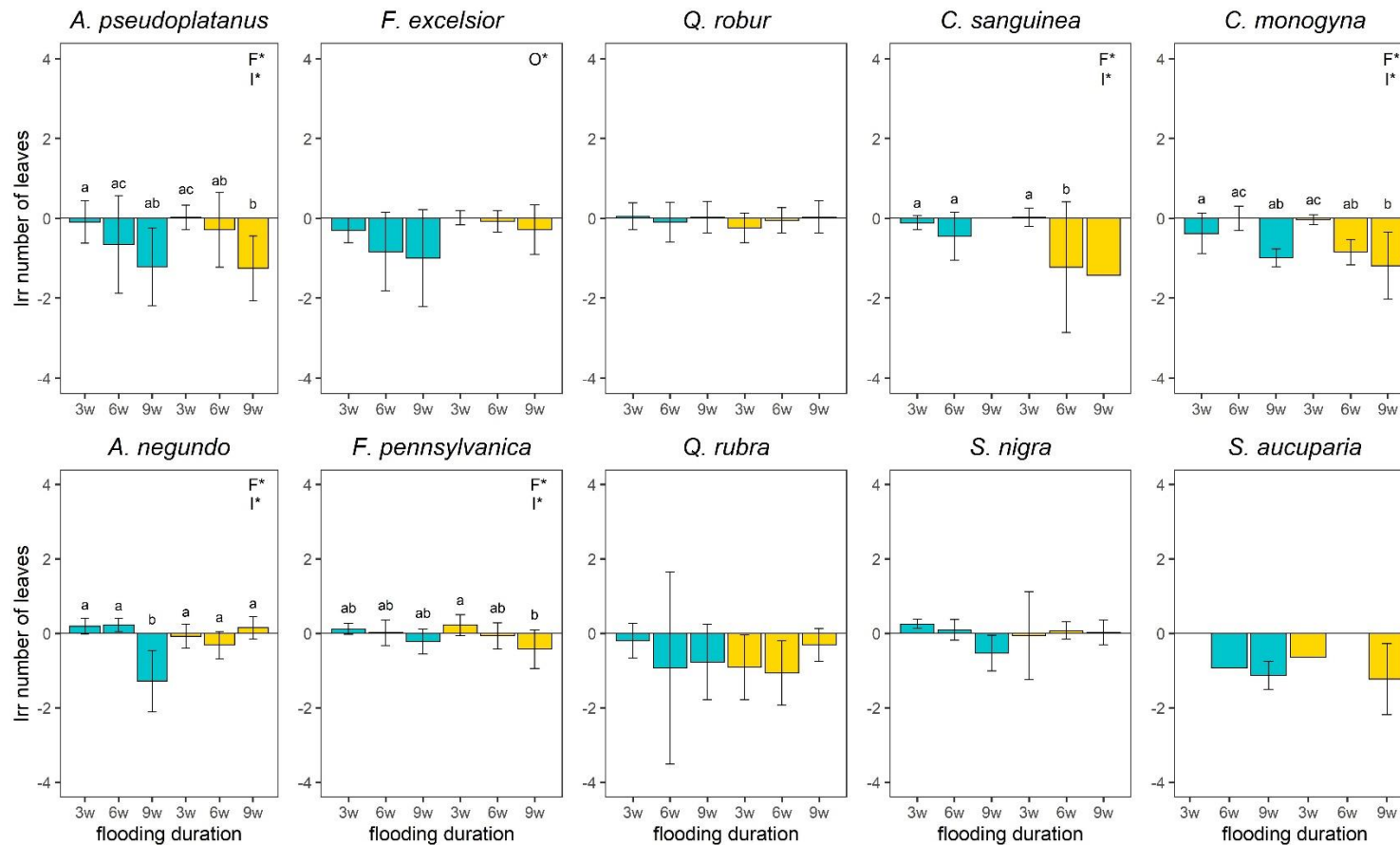


Fig. 3.5 Logarithmic response ratio (Irr) of number of leaves of the species depending on the treatments 12 weeks after the experiment started. w = weeks, the number prefixed indicates the flooding duration in weeks; Blue boxplots: aeration, yellow boxplots: no aeration; significant differences between the main effects were marked with capital letters in the upper right corner (F\* – Flooding duration, O\* – Oxygen treatment, I\* – Interaction between both); Effects of treatments on survived plants were considered significant (i.e different from the control) when 95% CI did not overlap with zero. Missing bars represent groups with a mortality of 100%. Missing CI represent groups with only one survival individual.

## Stem diameter

For nearly all treatments, there were significantly negative flooding effects on the stem diameter compared to the control for *C. sanguinea*, *A. negundo*, *C. monogyna* and *Q. rubra* (Fig. 3.6). In contrast, the species *F. excelsior*, *F. pennsylvanica* and *S. nigra* showed significantly positive flooding effects on the stem diameter for most flooding treatments compared to the control. *A. pseudoplatanus* and *Q. robur* showed no differences in stem diameter (Fig. 3.6). The negative flooding effects increased from short to medium flooding duration for *C. sanguinea* ( $p$ -value = 0.025) and from short to long flooding duration for *C. monogyna* ( $p$ -value = 0.017). The stem diameter of *Q. robur* decreased significantly with aeration compared to the treatments without aeration ( $p$ -value = 0.012; Fig. 3.6).

The flooding tolerant species showed a marginally positive flooding effect on the stem diameter compared to the flooding intolerant species ( $p$ -value = 0.046). The stem diameter of the native species increased significantly more with flooding than of the non-native species ( $p$ -value = 0.022; Fig. 3.6)

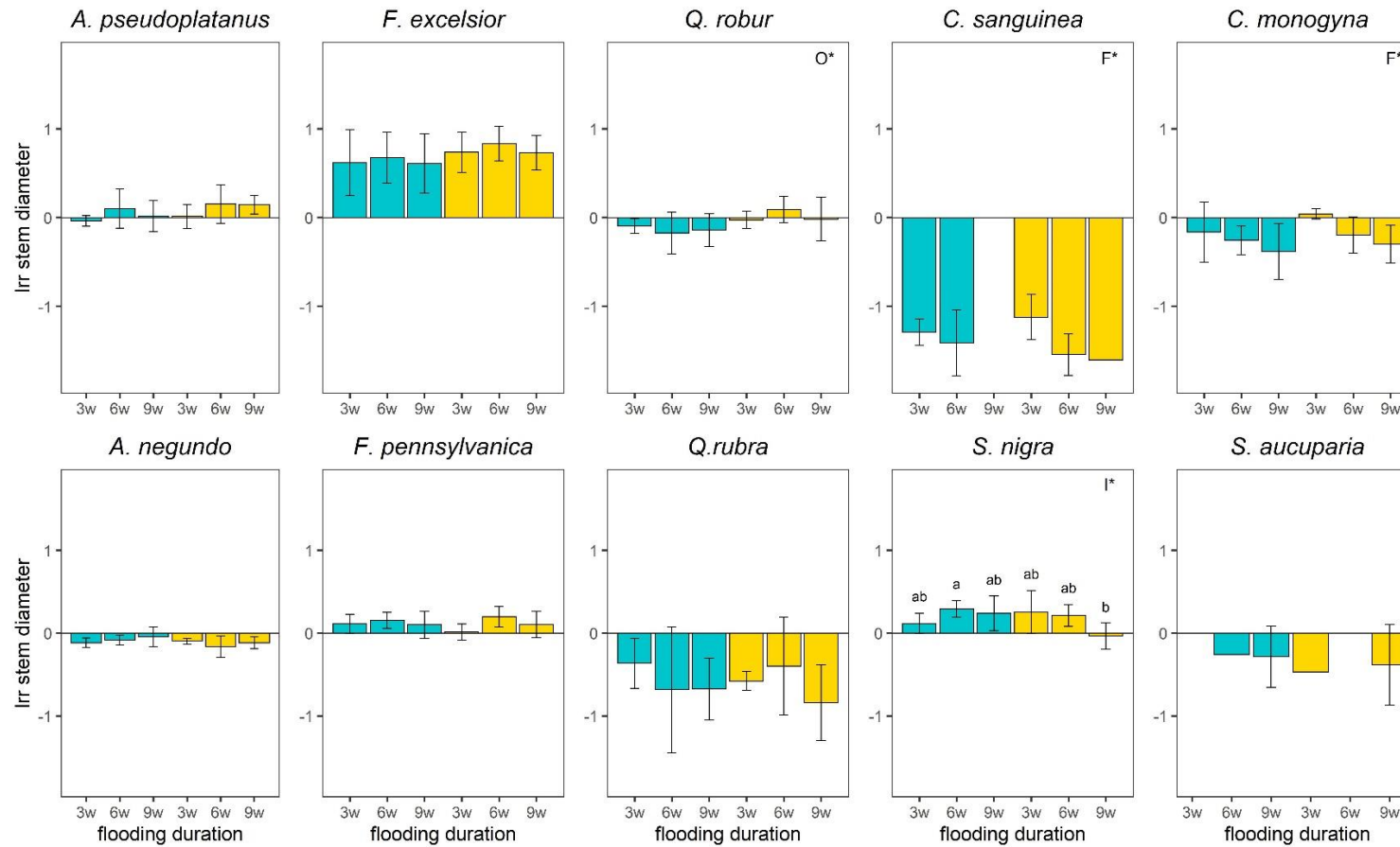


Fig 3.6 Logarithmic response ratio (Irr) of the stem diameter of the species depending on the treatments 12 weeks after the experiment started. w = weeks, the number prefixed indicates the flooding duration in weeks; Blue boxplots: aeration, yellow boxplots: no aeration; significant differences between the main effects were marked with capital letters in the upper right corner (F\* – Flooding duration, O\* – Oxygen treatment, I\* – Interaction between both); Effects of treatments on survived plants were considered significant (i.e different from the control) when 95% CI did not overlap with zero. Missing bars represent groups with a mortality of 100%. Missing CI represent groups with only one survival individual.

## Discussion

As expected, the sapling foliar injury of most studied species increased with increasing flooding duration. Furthermore, the flooding tolerant species developed better in terms of survival and foliar injury than the flooding intolerant species after flooding. For example, *A. negundo* and *F. pennsylvanica*, both classified as highly flooding tolerant in literature (Kozlowski, 1984; Tang & Kozlowski, 1984), possess typical adaptations to flooding such as the formation of lenticels and adventitious roots that appear very quickly after five days of flooding (Tang & Kozlowski, 1984). Due to these adaptations, both species showed the best survival and least foliar injury in our study and therefore could pose a risk to native species in alluvial forests. The differences in species response to flooding can be explained mainly by their ability to react to the resulting stress with morphological, physiological and metabolic adaptations, irrespective whether they are native or non-natives (Glenz et al., 2006; Hook & Brown, 1973). This may explain why only a few individuals of *S. aucuparia* survived the flooding treatments compared to a 100% survival rate of the control. This species does not develop any of the adaptation structures such as lenticels, aerenchyma or adventitious roots (Glenz et al., 2006). Our findings were also consistent with the studies of Brink (1954) and Kozlowski (1984), who classified *S. aucuparia* as intolerant even to short flooding events. The same reason could explain the lower survival rate of *C. sanguinea* compared to *F. excelsior* and *Q. robur*. *C. sanguinea* is only capable of forming adventitious roots, while the other two species can additionally form lenticels and aerenchyma (Frye & Grosse, 1992; Kozlowski, 1997; Siebel, 1998). Siebel & Bouwma (1998) demonstrated that saplings of *C. sanguinea* occur only in the higher areas of the hardwood floodplain forest. In addition, not only the formation of these morphological structures is important, but also their quantity (Colin-Belgrand et al., 1991). Colin-Belgrand et al. (1991) observed that *Q. robur* and *Q. rubra* developed both, lenticels and adventitious roots but with a significantly higher intensity for the flooding tolerant and native species *Q. robur*. Furthermore, the non-native *Q. rubra* is not a typical alluvial forest species and is classified as flooding intolerant (Colin-Belgrand et al., 1991), an assessment that is – despite its ability to form lenticels and adventitious roots – supported by the high mortality rate and foliar injury in the present study. For this reason, *Q. rubra* seems to be unable to establish successfully in alluvial floodplain forests and therefore does not pose a risk to native species in alluvial forests. However, we have to take into account that it is difficult to assess invasion impacts because changes in species composition can be slow (Crooks, 2005; Strayer et al., 2006) and might take many years before any effects become apparent (Chabrierie et al., 2010). On the other hand, it

was striking that also many individuals from *Q. rubra* died even in the control after one year. Generally, *Q. rubra* is not exposed to many abiotic risks except for the risk of late frost. It is more likely that gnawing by rabbits or other rodents caused the mortality. In addition, fungal pathogens for example *Pezizula cinnamonea* or root damage due to parasites like *Gymnopus fusipes* could have led to this high mortality (Kehr, 1991).

In general, there are contrary opinions about the flooding tolerance for many species. For the species investigated in this study, the greatest differences in literature were observed for *S. nigra*. In our study, all individuals of *S. nigra* survived the flooding event, independent of the flooding duration, but showed a high mortality rate and foliar injury after one year. In contrast, the individuals of the control showed a high survival rate and less foliar injury even after one year. In many studies, *S. nigra* is described as flooding intolerant (Glenz, 2005; Hoag & Landis, 2001; Westhus, 1986). In contrast, the work of Tremolieres et al. (1998), classified *S. nigra* as flooding tolerant. Those controversial and contrary assessments show that there are many factors influencing flooding tolerance. Regardless of the abiotic factors such as the “timing”, “depth” and “frequency” of flooding and its biotic factors such as the “developmental stage” of the individuals (Glenz et al., 2006), possibly the biggest problem in most studies is that the classification of the flooding tolerance was based on the observations being made during or immediately following the stress period (Malik et al., 2002; Striker, 2012). Most authors of other studies did not include a recovery phase (Striker, 2008). As we can see in our study, the conclusions drawn may change after a certain recovery period. For example, we also observed a high mortality rate for *A. pseudoplatanus*, *F. excelsior*, *Q. robur* and *Q. rubra* after one year. After flooding, plants can face compounding stress factors leading to an increase injury or death (Striker, 2012). Depending on the growth pattern of the species, flood damage effects may be present up to two years after flooding and therefore recovery time may result in an additional weakening of these species (Glenz et al., 2006). Another example of the different classifications with regard to flooding tolerance and the importance of the inclusion of a recovery period can be shown for *C. monogyna*. Again, there are contrary judgments, because *C. monogyna* was partly described as a species with a low flooding tolerance by Glenz (2005), while Vreugdenhil et al. (2006) described this species as having a higher flooding tolerance than *F. excelsior* and *Q. robur*. However, the ability of *C. monogyna* to cope with flooding is poorly understood, although it has been shown to be able to recover better after flooding when compared to *F. excelsior* and *Q. robur* (Frye & Grosse, 1992). This is in accordance with our study, which also showed a higher foliar injury for *C. monogyna* compared to *Q. robur* and *F. excelsior* in the long flooding duration after twelve weeks but less foliar injury and better



survival rates than both species after the recovery period of nine months. A poor performance during flooding does not necessarily involve a reduced flooding tolerance, as some species can save energy for later recovery (Striker, 2012). Again, the inclusion of a certain long recovery period seems to be very important for the assessment of flooding tolerance.

When reviewing the growth of the studied species, there were many species, which showed a negative flooding effect on plant height. In literature, the most significant effect found in shrubs and trees affected by flooding is a decline in shoot growth (Blom et al., 1994; Ewing, 1996; Frye & Grosse, 1992; Gravatt & Kirby, 1998; Kozłowski, 1984). The species may temporarily suspend their growth during flooding by slowing down their metabolism, thus saving energy and maintaining high carbohydrate reserves (Striker, 2012). The fact that the flooding intolerant species *A. pseudoplatanus* and *Q. rubra* showed no differences in plant height compared to the control could indicate that this adaptation strategy is not present in these species. Instead, they show a high mortality rate. In accordance to Frye & Grosse (1992), we found no differences in plant height during a partial flooding of up to nine weeks compared to the controls for the flooding tolerant species *F. excelsior* and *Q. robur*. For those species, growth appears to slow down only when flooding continues for longer periods (Alaoui-Sossé et al., 2005). For *A. negundo*, we could observe a trend towards a greater plant height with increasing flooding duration. In the study by Kozłowski (1984), *A. negundo* showed a higher plant height compared to the unflooded control. One mechanism for a higher plant height could be an enhanced shoot elongation, which allows the plants to extend their leaves out of the water and thereby remain in contact with the atmosphere (Kozłowski, 1997).

In general, with an increased flooding duration, many species react with a decreased number of leaves, which is in accordance with other references (Frye & Grosse, 1992). This reaction could be an adaptive strategy by losing especially older leaves to save energy, which can be used for survival (Mommer & Visser, 2005). On the other hand, leaf loss could also be an indicator that the plants are suffering very badly under flooded conditions. Across all flooding durations, no changes in the number of leaves were observed for *Q. robur*. This is in accordance with the studies of Alaoui-Sossé et al. (2005) and Frye & Grosse (1992). The reason could be, as Späth (1988) documented, that *Quercus* saplings were able to sprout new leaves even after being flooded for more than 50 days in the Rhine flood in 1987. No differences in the number of leaves compared to the control were also visible for *F. excelsior*, *F. pennsylvanica*, *Q. robur* and *C. sanguinea*. In response to flooding, some species are also able to produce new leaves with a thinner cell wall and cuticle thickness in order to reduce gas diffusion resistance (Frost-

Christensen et al., 2003). Another reason for no change in the number of leaves might be that the root system was more affected by the flooding than the leaves.

The flooding tolerant species showed a significantly higher secondary growth compared to the flooding intolerant species. This phenomenon was often observed in flooding tolerant species as they produce more intercellular spaces and lenticels to enhance oxygen transport (Frye & Grosse, 1992; Kozłowski, 1997; Roloff, 2010). This is also the reason, why there was a significantly higher secondary growth for mostly all treatments compared to the control for *F. excelsior* and *F. pennsylvanica*. Surprisingly, *A. pseudoplatanus* also showed a higher secondary growth for the long flooding duration, which contrasted the study of Frye & Grosse (1992) who observed a significantly lower secondary growth after 120 days of flooding for the same species. However, in this study, *A. pseudoplatanus* was only flooded up to nine weeks. Analogously, two of the flooding tolerant species, *C. monogyna* and *C. sanguinea* that are not capable of forming aerenchyma or lenticels showed a significantly lower secondary growth compared to the control, which was also visible for the flooding intolerant species *Q. rubra* (Frye & Grosse, 1992). These species may have stopped secondary growth to save energy.

Although there are statistical differences between the two oxygen treatments, these rather small differences do not seem to have ecological importance for most of our study species. In general, there was no clear noticeable pattern towards survival, foliar injury and growth. An exception is *Q. robur*, which showed a significantly larger secondary growth over all flooding durations without aeration. This may suggest that lenticels were developed even faster in the treatment with a lower oxygen content due to more anaerobic conditions (Frye & Grosse, 1992). This would be consistent with the observed enlarged lenticels and thus a higher secondary growth even after three weeks of flooding in the study of Colin-Belgrand et al. (1991). The early formation of morphological structures under more anaerobic conditions could also be responsible for less leaf loss of *F. excelsior* in the treatment without aeration. The reason for the rather small differences in oxygen content between the oxygen treatments itself, may be that the temperature dependent oxygen solubility in water is resulting in a decreased oxygen content of all basins during summer irrespective of aeration (Colmer et al., 2011). In addition, the oxygen content may decrease in all basins with increasing flooding duration because of the activity of microorganisms, which consume oxygen. On the other hand, all basins were set outside, which could also have introduced oxygen even to the basins without aeration due to wind turbulences and the refilled freshwater as it evaporates. Furthermore, the lowest oxygen

value of  $3.1 \text{ mg} \cdot \text{l}^{-1}$ , was only minimal below the critical oxygen value for fishes and thus possibly not low enough to determine ecological effects on the development of our plants.

## Conclusion

Overall, the typical alluvial floodplain forest species that are classified as flooding tolerant developed better in terms of survival and injury after flooding. This result was also found in the comparison of native and non-native saplings within a genus. Due to the complexity of interacting processes, the knowledge about flooding tolerance of many tree and shrub species is quite sparse and, in some cases, contradictory. However, both flooding tolerant and flooding intolerant species present response patterns that are influenced not only by flooding duration and oxygen content but also by other factors such as seasonal timing, depth and frequency of flooding, as well as the developmental stage of the individuals (Glenz et al., 2006). Furthermore, plant recovery after flooding seems to be very important to avoid misjudgements in the assessment of flooding tolerance of the species. In order to achieve a better and more comprehensive understanding of the flooding tolerance of woody species, laboratory experiments must be accompanied by field experiments. Nevertheless, experimental studies investigating long term flooding tolerance with regard to flooding duration are urgently required for floodplain forest management.

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## Competing Interest

The authors declare that they have no conflict of interest.

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## Appendix Chapter 3

Tab. A3.1 Stratification procedure of the ten study species.

Year			2016	2016	2016	2016	2016	2016	2016	2016	2017	2017	2017	2017	2017	2017	2017	2017	2017	2017	2017	2017	2017	2017	2017	2017
Month			11	11	11		12	12	12		1	1	1	1		2	2	2		3	3	3		4	4	4
Week			45	46	47	48	49	50	51	52	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Species	soaked	heat at 42°C																								
<i>A. negundo</i>																										
<i>A. pseudoplatanus</i>																										
<i>C. sanguinea</i>	24 h																									
<i>C. monogyna</i>	24 h																									
<i>F. excelsior</i>	24 h																									
<i>F. pennsylvanica</i>	24 h																									
<i>Q. robur</i>		2 h																								
<i>Q. rubra</i>		2 h																								
<i>S. nigra</i>	24 h																									
<i>S. aucuparia</i>	24 h																									

	stored at 25°C
	freezed at -5°C
	stored at 4°C

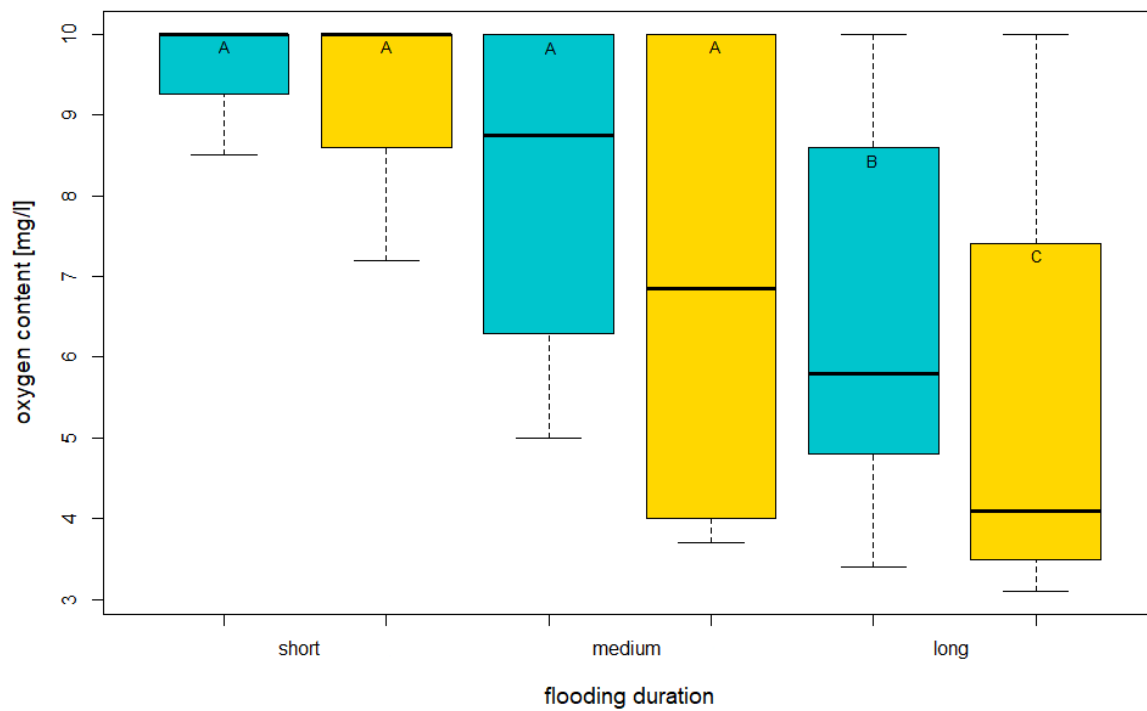


Fig. A3.1 Oxygen content of water in mg/l of the flooding basins depending on the treatments. Flooding duration short = 3 weeks, medium = 6 weeks, long = 9 weeks; blue boxplots stand for oxygen supply by aeration, yellow boxplots stand for no aeration; Letters indicate significant differences in oxygen content.

Tab. A3.2 Oxygen content [mg/l] of the flooding basins during the test duration. FD = flooding duration: short = 3 weeks, medium = 6 weeks, long = 9 weeks. O<sub>2</sub> = oxygen supply by aeration; w =week and - means, that no more measurements were done because flooding treatment had finished; \* indicate significant differences in oxygen content of the corresponding flooding duration or oxygen treatment.

Flooding basins			Oxygen content [mg/l]								
Treat-ment	FD	O <sub>2</sub>	w 1	w 2	w 3	w 4	w 5	w 6	w 7	w 8	w 9
1	short*	yes	10	10	8.5	-	-	-	-	-	-
2		no	10	10	7.2	-	-	-	-	-	-
3	medium	yes	10	10	8.9	8.6	6.3	5	-	-	-
4		no	10	10	6.9	6.8	4	3.7	-	-	-
5	long*	yes*	10	10	8.6	8.3	5.8	5	4.8	3.4	4.5
6		no*	10	10	7.4	7	3.7	3.1	4.1	3.1	3.5



## **Chapter 4**

No evidence for flooding stress memory in saplings of eight hardwood floodplain forest species

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## Abstract

Alluvial floodplain forests became rare in many parts of Europe, due to anthropogenic changes. Therefore, restoration of floodplain forests is important, but a difficult task because of the complex environmental conditions. The zonation of woody species in floodplains is mainly determined by hydrological conditions, not only within one year but also during the previous years. Tolerance to flooding can be regarded as a key factor for the successful establishment. We examined whether a previous flooding showed an increased flooding tolerance of saplings from eight woody floodplain forest species after a recurrent flooding under controlled common garden conditions at the research station Gießen-Leihgestern (Germany). This would indicate a stress memory towards flooding stress. The individuals of the experiment already experienced a partial flooding of three different durations (three, six or nine weeks) or no flooding in the previous year. After nine months of recovery, these fourteen-months-old saplings were again either exposed to a partial flooding of nine weeks or no flooding. We assessed foliar injury and growth in terms of plant height, number of leaves and stem diameter three weeks (short-term recovery) and nine months (medium-term recovery) after flooding. The saplings showed no increased tolerance to a recurrent flooding irrespective of the previous experienced flooding duration. Therefore, no immediate stress memory towards flooding stress could be observed. To recover after flooding seems to be the better option compared to forming a stress memory, which explained that most species showed a decreased foliar injury after medium-term compared to short-term recovery period.

## Introduction

Floodplains form the transitional area between aquatic and terrestrial ecosystems along rivers (Richardson et al., 2007). The high small-scale heterogeneity results in an exceptionally high biodiversity (Tockner and Stanford, 2002). In general, softwood floodplain forests can be found at sites with more frequent and prolonged flooding compared to hardwood floodplain forests, which are flooded less frequently and for shorter periods in Central Europe (Alaoui-Sossé et al., 2005).

Due to anthropogenic actions, such as building dikes, hardwood-floodplain forests are highly endangered ecosystems in many parts of Europe (Brunotte et al., 2009). In addition, altered

dynamics of riparian ecosystems often led to strong changes in species composition and seem to trigger the establishment of non-native tree species (Hood & Naiman, 2000; Rood et al., 2003). On top of this, climate change impacts on alluvial plant communities add to the uncertainty about adequate conservation and restoration measures in these habitats (Mosner et al., 2015). Therefore, the restoration of floodplain forests is needed to establish and preserve riparian biodiversity (Brunotte et al., 2009).

Flooding leads to water saturation of soil pores, causing substantial stress to terrestrial plants especially during the growing period (Leyer, 2004). Thus, species that grow in floodplains must be adapted to changing water levels (Glenz et al., 2006) and flooding tolerance is certainly the key factor for these species to persist (Toner & Keddy, 1997). Due to the low solubility and diffusion rates of oxygen in water, flooded plants experience hypoxic or anoxic conditions at their roots (Streng et al., 1989). Reduced oxygen availability leads to reduced photosynthesis (Streng et al., 1989), which in turn declines growth rate and biomass production and increases the injury to the flooded plants (Bockelmann et al., 2002).

Riparian plant species have developed different mechanisms to tolerate flooding (Du et al., 2012; Vreugdenhil et al., 2006). Most adaptations are morphological structures (Streng et al., 1989), such as hypertrophied lenticels, adventitious roots and aerenchyma tissues. Those structures increase the oxygen uptake and transport into the root system under flooded conditions (Cavers & Harper, 1967). In scientific literature, conclusions on flooding tolerance have been mostly based on the responses during or immediately after the stress period. In contrast, long-term effects beyond the immediate impact of flooding are often neglected (Glenz et al., 2006). Indeed, flooding tolerance is the ability to survive flooding and to acclimate afterwards and must be thereby determined after a certain recovery period (Crisp et al., 2016; Schindler et al., 2020).

Flooding tolerance increases with age and developmental stage of the plants, respectively (Hauschild & Hein, 2009). They are less sensitive towards flooding later in life and grow above the water level. Thus, species considered as flooding tolerant might be quite vulnerable to flooding during early establishment (Streng et al., 1989).

It has been shown that plants can form stress memories after stress events (Tahkokorpi et al., 2007; Walter et al., 2011), which can be defined as structural, genetic, and biochemical modification in plants (Fleta-Soriano & Munné-Bosch, 2016). Those stress memories have been revealed as one mechanism for ecological and evolutionary success of plants to be prepared for

future stress (Bruce et al., 2007). Some plant species are less negatively affected by environmental stress when they have already experienced the same stress earlier in their life (Crisp et al., 2016). Although, an increased tolerance to the same stress may compromise plant productivity in short-term, for example through a reduction of photosynthesis, it can lead to an increased tolerance to subsequent stress and therefore favor productivity in long-term (Bruce et al., 2007). Whether and when such memories would favor plants depend not only on the species, but also on the duration and severity of the stress to which the plants are exposed (Fleta-Soriano & Munné-Bosch, 2016). For example, when the stress is too severe, productivity may also be negatively affected in both short- and long-term. In addition, there is an evidence that plants either are able to form stress memories or to recover after stress (Crisp et al., 2016; Goh et al., 2003). The latter would have a positive effect under unpredictable environmental conditions. The key role of this process seem to anchored in the RNA turnover, which can either facilitate recovery by clearing the stress-responsive transcriptome or by permitting memory formation by selectively stabilizing transcripts (Crisp et al., 2016).

To summarise, flooding tolerance depends on many different factors. Therefore, the success of restoration projects requires knowledge on the ecological, hydrological and geomorphological processes, as well as the flooding tolerance of the typical species (Streng et al., 1989). In addition, the question arises, whether there is a memory towards flooding stress for the investigated species and whether they are more likely formed after a certain flooding duration. Consequently, we investigated whether fourteen-months-old juveniles of eight hardwood floodplain forest species tolerate flooding better when they have already experienced flooding in the previous year. To this end, we examined the influence of a recurrent flooding on the short- and medium-term foliar injury and growth of juveniles under controlled common garden conditions. Specifically, we tested the following hypothesis in a greenhouse experiment:

1. Individuals will tolerate a flooding better (i.e. lower short- and medium-term foliar injury and higher growth in terms of plant height, number of leaves and stem diameter), when they already experienced a flooding the previous year.
2. There is a higher flooding tolerance (i.e. lower short- and medium term foliar injury and higher growth in terms of plant height, number of leaves and stem diameter) the longer the previous flooding lasted.

## Methods

### Study species

As representatives for flooding tolerant hardwood floodplain forest species of northern Central Europe, we selected *Quercus robur* L., *Fraxinus excelsior* L., *Cornus sanguinea* L. and *Crataegus monogyna* JACQ. (Tab. 4.1). We also included the less flooding tolerant species *Acer pseudoplatanus* L. and *Sambucus nigra* L., which often occur in higher elevated hardwood floodplain forests (Tab. 4.1). In addition, we tested *Acer negundo* L. and *Fraxinus pennsylvanica* MARSHALL, both native to North America, but also occurring in some hardwood floodplains in Central Europe.

Tab. 4.1 Information about study species, their family and flooding tolerance (including citations). The nomenclature of plant species follows Rothmaler et al. (2017).

<b>Species</b>	<b>Family</b>	<b>Flooding tolerance</b>
<i>Acer negundo</i>	Sapindaceae	high (Starfinger et al., 2011)
<i>Acer pseudoplatanus</i>	Sapindaceae	low (Siebel & Bouwma, 1998)
<i>Cornus sanguinea</i>	Cornaceae	intermediate (Glenz, 2005)
<i>Crataegus monogyna</i>	Rosaceae	intermediate (Siebel & Bouwma, 1998)
<i>Fraxinus excelsior</i>	Oleaceae	high (Glenz, 2005)
<i>Fraxinus pennsylvanica</i>	Oleaceae	high (Tang & Kozłowski, 1984)
<i>Quercus robur</i>	Fagaceae	high (Glenz, 2005)
<i>Sambucus nigra</i>	Adoxaceae	low (Glenz, 2005)

## Experimental setup

In autumn 2016, seeds of the study species were collected from trees in the active and former floodplain along the Middle Elbe River (in a range of NW 53° 21' N, 10° 42' E and SE 52° 58' N, 11° 38' E). After stratification, they were sown and grown in a greenhouse during April and May 2017 at the research station Linden-Leihgestern of the Justus-Liebig University (Giessen, Hesse/Germany, 50°32'N, 8°41'E). At the end of May, all emerged saplings were planted into pots (6 cm x 6 cm x 7.5 cm) and filled with a 1:1 mixture of sand and commercial potting soil (Fruhstorfer Erde®, Type P, Industrie-Erdenwerke Archut GmbH, Lauterbach/Germany). This soil is suitable especially for juveniles and provides standardized substrate in the experiment. Afterwards, they were set up outdoors on a paved area exposed to ambient light, wind, temperature and precipitation. During summer 2017, when the saplings were six weeks old, they were subjected to an experimental flooding with different flooding durations ( $k = 4$ ): no, short (three weeks), medium (six weeks) and long (nine weeks; Fig. 4.1a). Therefore, the saplings were randomly assigned to basins of the corresponding flooding duration and covered with tap water until 2 cm above the pot rim, i.e. plants were not completely submerged. Twelve weeks after the experiment started, including a recovery period of at least three weeks for the longest flooding duration, foliar injury and growth in terms of plant height, number of leaves and stem diameter were recorded. The foliar injury was documented using five injury classes (1: all leaves undamaged, 2: all leaves fully developed but show damage < 50%, 3: leaves not fully developed and damaged > 50%, 4: all leaves damaged or dead, but plant is still alive, 5: plant dead). For medium-term recovery, foliar injury was additionally recorded after nine months recovery, which was just before the recurrent flooding started in 2018 (Fig 4.1b). In the meantime, the plants were repotted into larger pots (11 cm x 11 cm x 12 cm) and watered as needed to ensure optimal conditions during their recovery period. For more details on the first flooding experiment, see (Schindler et al. 2020).

During summer 2018, the fourteen-month-old saplings were subjected to a new flooding. The factor levels were either nine weeks of flooding or no flooding ( $k = 2$ ; Fig. 4.1c). Due to mortality of the first flooding experiment, altogether 348 individuals were available for the second flooding experiment, i.e. 48 individuals each of *A. negundo*, *C. monogyna* and *F. pennsylvanica*, 46 individuals of *Q. robur*, 44 individuals of *S. nigra*, 41 individuals of *A. pseudoplatanus*, 40 individuals of *C. sanguinea* and 33 individuals of *F. excelsior*.

From June to September 2018, the experiment was set up outdoors on the same paved area as in the previous year. Altogether, six flooding basins comprising of wooden frames of 1.5 m<sup>2</sup> lined with a 0.2 mm thick waterproof silage film (with the bright side upwards) were prepared of which three of them were flooded nine weeks (flooded treatment) and three of them were not flooded (unflooded treatment). This setup resulted in a split-plot design, i.e. each treatment was located in one block (i.e. basin) thrice to ensure manageability and repetitions. The treatment groups were randomly assigned to the six basins. Within each basin, we allocated approximately the same number of plants from all previous flooding durations and from the unflooded control. The pots were randomly distributed within the basins and positions were changed every three weeks. The flooded basins were again filled with tap water up to 2 cm above the pot rim. To counteract uplift the pots were weighted with stones. When necessary, evaporated water was refilled to keep the water level constant during the flooding period. Pots in unflooded treatment basins were regularly irrigated to keep the soil constantly moist.

At the beginning (June 14<sup>th</sup> 2018) and after a short-term recovery period of three weeks after the completion of the experiment (September 6<sup>th</sup> 2018), foliar injury and growth in terms of plant height, number of leaves and stem diameter were recorded. The height of the plants was determined by measuring the distance between root collar and terminal bud. In addition, the number of leaves was counted and the stem diameter at the soil surface was measured using calipers. Afterwards the differences ( $\Delta$ ) between plant height, number of leaves and stem diameter from before to after the experiment were calculated. Due to leaf loss or the death of upper shoots, negative values could occur. If several stems existed, the sum stem diameter was used. As in the previous year, foliar injury was assessed using a scale with five classes. In June 2019 foliar injury was recorded again after a medium-term recovery period of nine months (Fig. 4.1d).

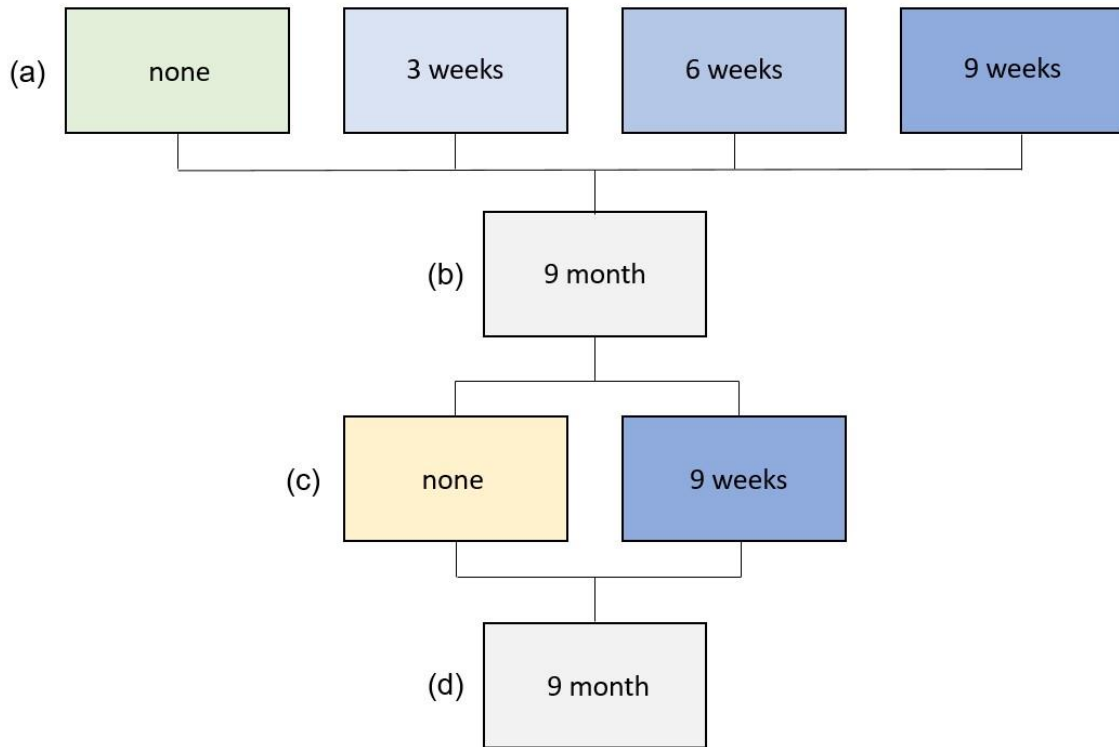


Fig. 4.1 Study design (a) previous flooding duration, (b) previous recovery time, (c) new flooding treatment, (d) recovery time.

## Statistical analyses

We analyzed the effect of the ‘*previous flooding*’, the ‘*flooding duration*’ as well as the ‘*new flooding treatment*’ on the foliar injury of the saplings by conducting non-parametric Scheirer-Ray-Hare-Tests due to the fact that foliar injury was not normal distributed (Puri & Sen, 1985). As response variables, the parameters ‘*short-term foliar injury*’ and ‘*medium-term foliar injury*’ were used. We computed separate Scheirer-Ray-Hare-Tests for each species for both response variables with the factors ‘*previous flooding duration*’ (none, short, medium, long), the ‘*new flooding treatment*’ (yes, no) and their interaction (Crawley, 2007). For post-hoc testing, we used the Dunn Kruskal-Wallis multiple comparison with Benjamini-Hochberg adjusted *p*-values (Puri & Sen, 1985). To compare short- and medium-term foliar injury for each species, the response variable ‘*foliar injury*’ was used and separate Scheirer-Ray-Hare-Tests were calculated including the factor ‘*time*’ (3 weeks, 9 months).

We analyzed the effect of the ‘*previous flooding*’, the ‘*previous flooding duration*’ and the ‘*new flooding treatment*’ on the growth of the saplings by conducting several ANOVAs for split-plot designs (Crawley, 2007). As response variables, ‘ $\Delta$  *plant height*’, ‘ $\Delta$  *number of leaves*’ and



'*Δ stem diameter*' were used. Dead plants were excluded from the analyses to avoid the detrimental effects of zero values on the ANOVA results. Consequently, if there was a high mortality within a treatment, no *p*-values could be calculated. We computed separate ANOVAs for each species for all response variables with the factors '*previous flooding duration*' (none, short, medium, long) and '*new flooding treatment*' (yes, no) and their interaction. Those were nested in the factor *treatment* (summarized to two different treatments, where basins 1 – 3 were flooded and basins 4 – 6 were the unflooded treatment to ensure manageability) and included in the error term for the split-plot setup (Crawley, 2007). In order to calculate the relative contribution of each factor or each interaction to the total variance, the sum of squares of a factor or an interaction was divided by the total sum of squares (Crawley, 2007). We visually checked diagnostic plots to test the preconditions of ANOVAs (e.g. normal distribution, variance homogeneity; (Quinn & Keough, 2002). For the post-hoc pairwise t-tests Holm adjusted *p*-values were used (Crawley, 2007).

The significance level for all analyses was  $\alpha = 0.05$ . All statistical analyses and figures were carried out using the R software environment (R Development Core Team, 2017).

## Results

### Overview summarised for all species

In general, neither the previous flooding nor its duration showed an effect on the short- and medium-term foliar injury (Fig. 4.2). Only the newly flooded individuals showed a higher short-term and medium-term foliar injury, which means around one class worse compared to the unflooded treatment ( $p$ -value  $\leq 0.001$ ; Fig. 4.2). Overall, after medium-term recovery, foliar injury decreased of approx. half a class but varied over a greater range compared to short-term foliar injury (Fig. 4.2).

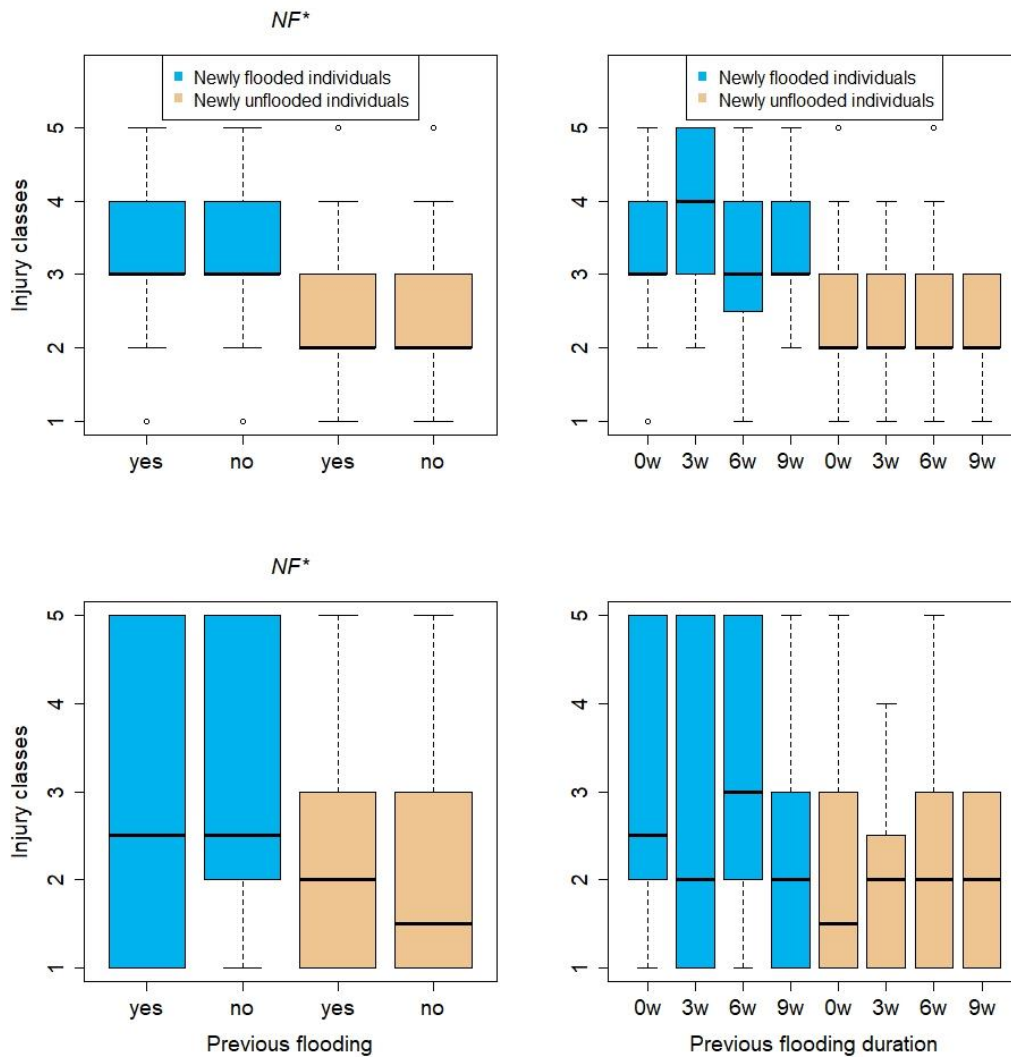


Fig. 4.2 Foliar injury summarised for all species depending on the previous flooding (left) and its duration (right) after short-term recovery of three weeks (top) and after medium-term recovery of nine months (bottom); Injury classes from 1 (without damage) to 5 (dead); w = weeks; Significant differences between the main effects are indicated with capital letters (PF\* - previous flooding, FD\* - previous flooding duration, NF\* - new flooding treatment).

With an averaged loss of six leaves, the  $\Delta$  number of leaves was slightly lower for the previously flooded individuals compared to no changes in leaf number for the individuals that experienced no flooding ( $p$ -value = 0.02; Fig. 4.3). Apart from that, the growth did not differ dependent on the previous flooding or its duration. The newly flooded individuals showed an almost constant plant height and lost up to 25 leaves, while the unflooded ones grew an average of three cm and did not show any changes in number of leaves ( $p$ -values  $\leq 0.001$ ; Fig. 4.3).

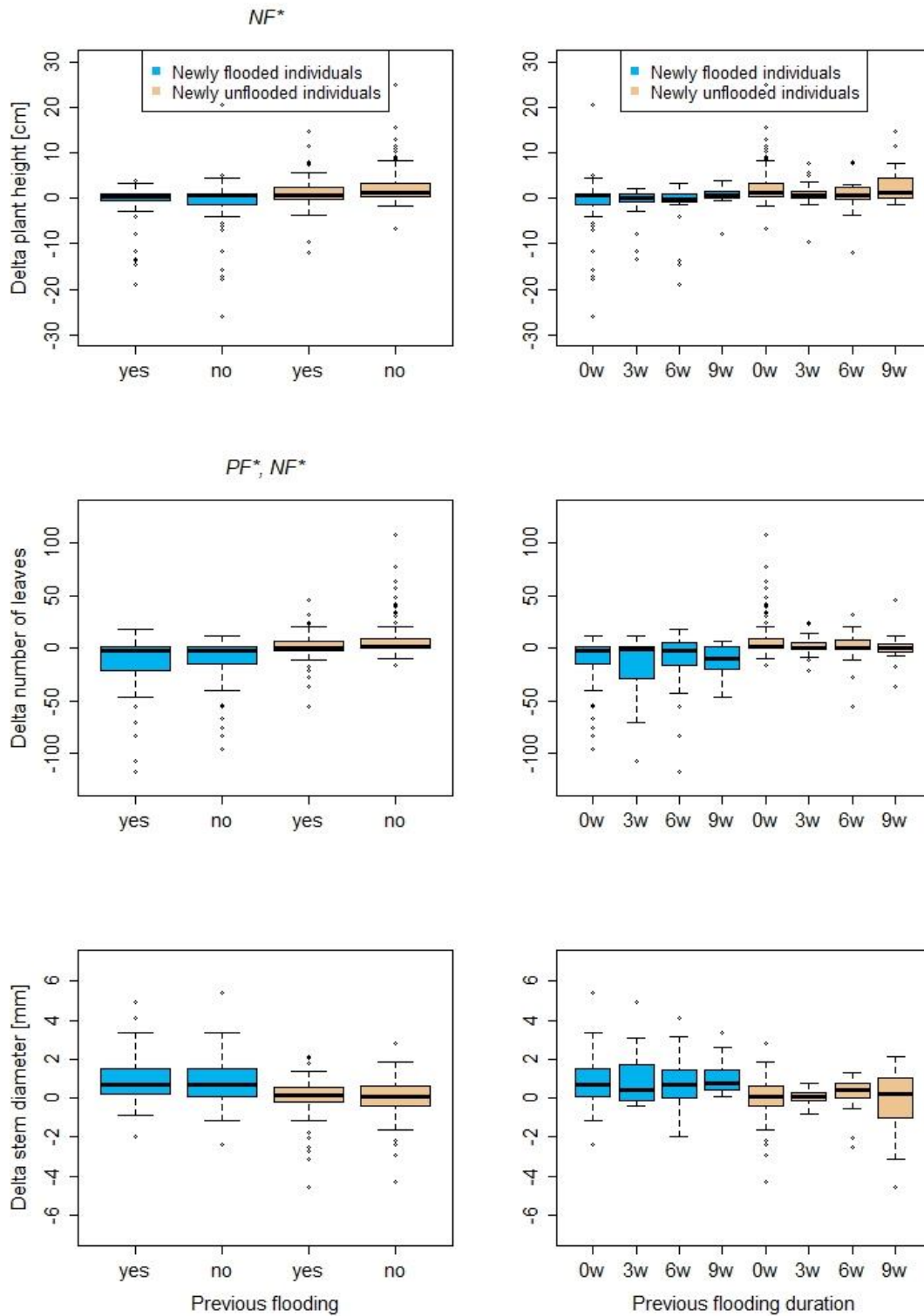


Fig. 4.3  $\Delta$  growth ( $\Delta$  plant height,  $\Delta$  number of leaves,  $\Delta$  stem diameter) summarised for all species depending on the previous flooding (left) and its duration (right) after short-term recovery of three weeks; w = weeks; Significant differences between the main effects are indicated with capital letters (PF\* - previous flooding, FD\* - previous flooding duration, NF\* - new flooding treatment).

## Species-specific differences in foliar injury

The newly flooded individuals of *A. pseudoplatanus* ( $p$ -value  $\leq 0.001$ ) and *F. excelsior* ( $p$ -value = 0.011) performed around one to one and a half injury classes worse compared to the unflooded individuals after short-term recovery. For *C. monogyna* they were classified around two classes worse after short-term ( $p$ -value  $\leq 0.001$ ) and around half a class worse after medium-term recovery ( $p$ -value = 0.005). All newly flooded *C. sanguinea* and *S. nigra* individuals showed a 100 % leaf damage or were even dead, while no or only less damage was visible for the unflooded individuals ( $p$ -values  $\leq 0.001$ ). In contrast, there was almost no leaf damage of the newly flooded individuals of *A. negundo* ( $p$ -value = 0.03), while most individuals of the unflooded treatment showed a low leaf damage of under 50 % after medium-term recovery (Fig. 4.4)

When comparing short- and medium-term foliar injury for the newly flooded individuals, the individuals of *A. pseudoplatanus* ( $p$ -value = 0.011) and *F. pennsylvanica* ( $p$ -value  $\leq 0.001$ ) decreased of around one class, *A. negundo* ( $p$ -value  $\leq 0.001$ ) and *F. excelsior* ( $p$ -value  $\leq 0.001$ ) of approx. one to two classes and *C. monogyna* ( $p$ -value  $\leq 0.001$ ) of two classes after nine months recovery (Fig. 4.4).

Overall, there were species-specific differences in foliar injury. For example, in the new flooding treatment, *A. pseudoplatanus* showed a higher foliar injury of around one class compared to *F. excelsior*, *A. negundo* and *F. pennsylvanica* ( $p$ -value  $\leq 0.001$ ), but approx. a half class lower compared to *S. nigra* and *C. sanguinea*, which showed the highest foliar injury of all species (Fig. 4.4).

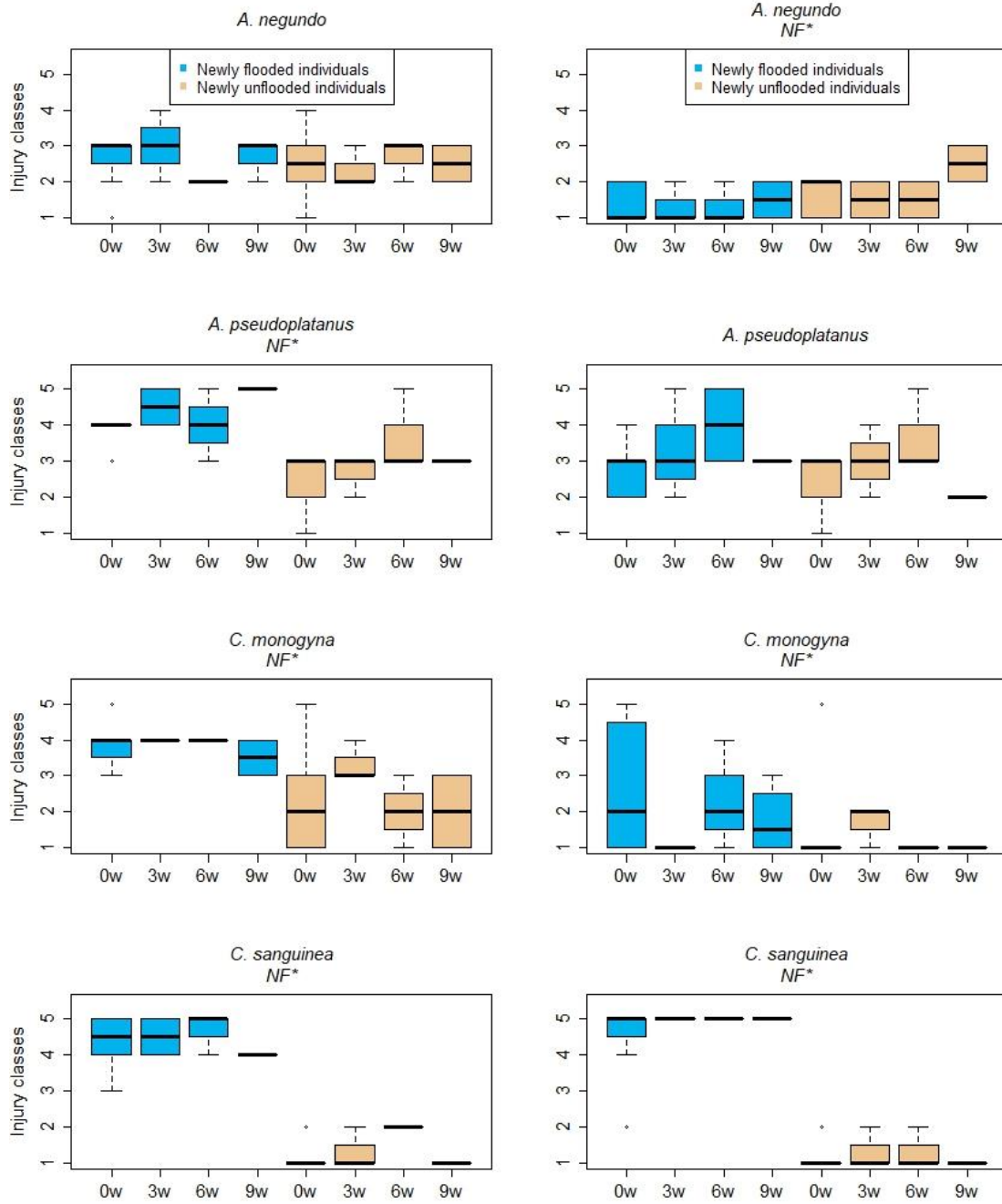


Fig. 4.4 Part 1

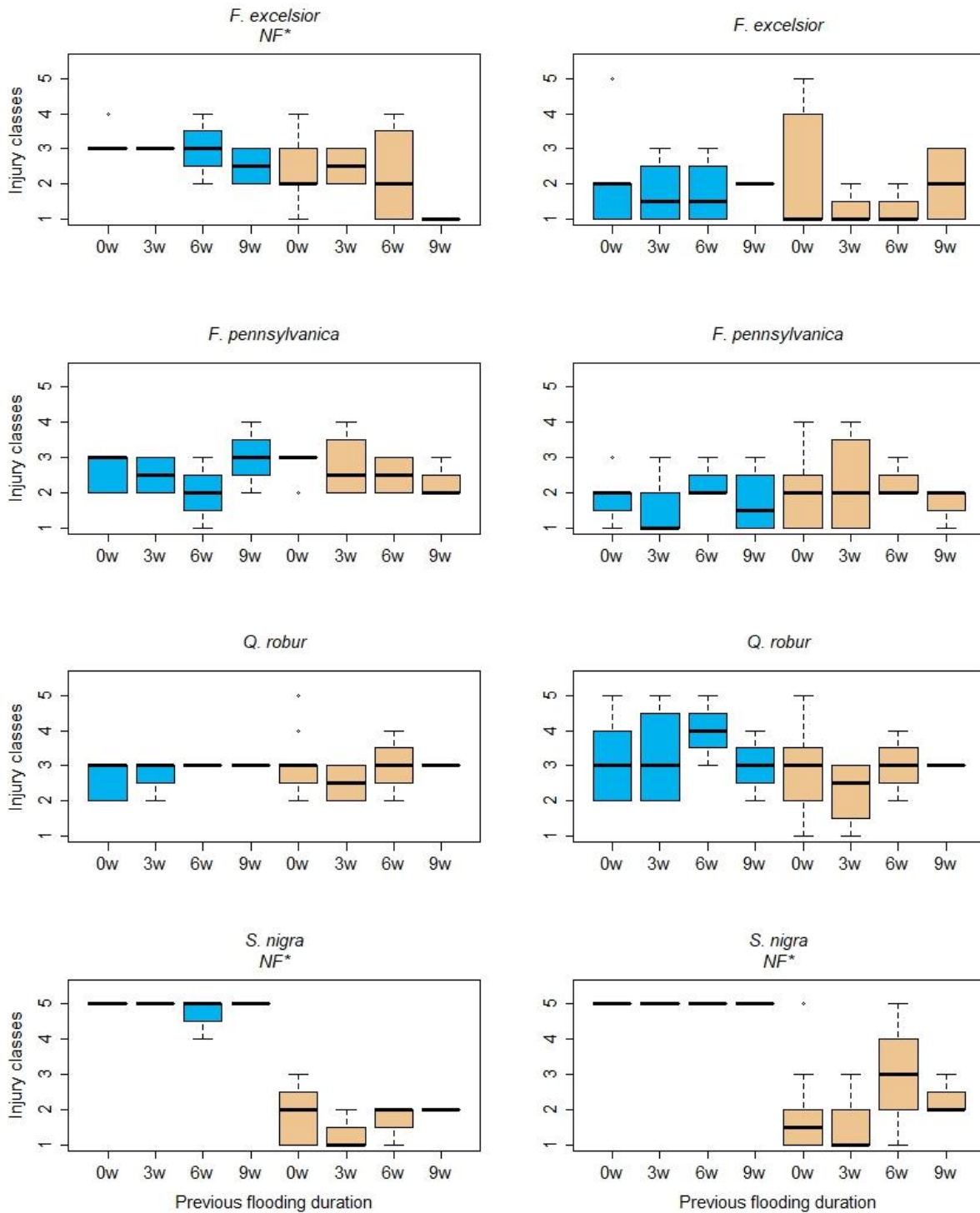


Fig. 4.4 Part 2 Foliar injury of each species depending on the previous flooding duration after short-term (left) and medium-term recovery of nine months (right); Injury classes from 1 (without damage) to 5 (dead); w = weeks; Significant differences between the main effects were marked with capital letters (PF\* - previous flooding, FD\* - previous flooding duration, NF\* - new flooding treatment).

## Species-specific differences in $\Delta$ growth

The previously flooded individuals of *F. excelsior* showed no change in number of leaves, while the previously unflooded ones showed an increase of averaged 6 leaves ( $p$ -value = 0.03). *C. sanguinea* ( $p$ -value = 0.037) had an approx. two mm lower  $\Delta$  stem diameter compared to the previously unflooded individuals (Figs. A4.2 and A4.3). There were no differences in  $\Delta$  growth parameter depending on the previous flooding or its duration for the other species.

The newly flooded individuals of *A. pseudoplatanus* ( $p$ -value  $\leq$  0.001), *C. monogyna* ( $p$ -value = 0.001) and *C. sanguinea* ( $p$ -value  $\leq$  0.001) showed a ten, five and ten cm lower  $\Delta$  plant height, respectively and a lower  $\Delta$  number of leaves of up to 60 leaves for *C. monogyna* compared to the unflooded individuals (Figs. A4.1 and A4.2). The newly flooded individuals of *F. pennsylvanica* showed a slightly lower  $\Delta$  number of leaves ( $p$ -value = 0.039) but a 2.5 mm higher  $\Delta$  stem diameter ( $p$ -value  $\leq$  0.001) compared to the unflooded ones (Figs. A4.2 and A4.3). A higher  $\Delta$  stem diameter of one to two mm for the flooded compared to the unflooded individuals was also visible for *A. negundo* ( $p$ -value  $\leq$  0.001), *F. excelsior* ( $p$ -value  $\leq$  0.001) and *Q. robur* ( $p$ -value = 0.003), while the reverse was true for *C. monogyna* ( $p$ -value = 0.004; Fig. A4.3).

## Discussion

Contrary to our expectations, both hypotheses must be rejected. The flooding tolerance in terms of foliar injury or growth of our investigated saplings did not improve due to a previous flooding or increasing flooding duration. Although it is widely accepted that plants have the capacity for what can be described as memory, in many instances, such memories cannot be observed. Ding et al. (2012) reported that multiple exposures to drought stress enable plants to respond to the same stress by more rapid adaptation compared to plants not previously exposed to drought stress. However, there is also evidence that such stress memories can have negative effects by hindering the recovery and therefore preventing the plant from maximizing growth as soon as favourable conditions occur (Crisp et al., 2016). Those negative effects were observed in particular in response to severe stress (Davies et al., 1992). For example in the study of Walter et al. (2011), severe drought stress in grasses resulted in biomass loss and reduction in photosynthesis when plants were challenged by a second drought, while Backhaus et al. (2014)

found out that mild drought stress seems to improve drought resistance of grassland species. Therefore, the stress level seems to be a decisive factor in whether a stress memory is formed or not.

On the one hand, the flooding stress of nine weeks alone could have been too severe for some species such as *C. sanguinea*, which showed a high injury and reduced growth after the new flooding treatment only. *C. sanguinea* also point out a high mortality and increased foliar injury with increasing flooding duration, after the first flooding (Schindler et al., 2020), probably because this species is only capable of forming adventitious roots (Glenz et al., 2006; Polomski & Kuhn, 1998). Therefore, the flooding of nine weeks alone, irrespective of previous flooding seems to damage the individuals of *C. sanguinea* to the extent that they are unable to recover. This fits to the study of Siebel & Bouwma (1998), who found that young shrubs of *C. sanguinea* only occur on high areas of the hardwood floodplain forests, which are flooded only a few days a year.

On the other hand, the nine weeks of flooding could have been too low for the highly flooding tolerant species such as *A. negundo* and *F. pennsylvanica*. They have the ability to form lenticels and adventitious roots very quickly after flooding (Hook & Brown, 1973; Tang & Kozłowski, 1984) and are able to survive flooding periods of up to 50% of their growing season without any damage (Zacharias & Breucker, 2008). This fast stress response would probably make a stress memory superfluous. Furthermore, we only repeated the flooding stress twice and not like Ding et al. (2012) several times. Possibly a memory is formed after several stress repetition. Another possibility would be that the probability to form a stress memory in long-lived trees increases in the course of life, just like flooding tolerance increases with age. Zweifel et al. (2020) for example found a delayed drought stress response in terms of restricted growth in mature pine trees after two to four year after drought. We only focused on the first two years of the establishment phase, which might be too short for final conclusions.

Furthermore, there appear to be two main strategies after stress events, where plants seem to balance between investing resources in stress memory or recovery from stress damage (Crisp et al., 2016). Flooding duration and –frequency are often unpredictable under natural conditions (Zhou et al., 2020). Hence, the predominant strategy for our species appear to recover after flooding, which seems to be the more successful option under unpredictable environmental conditions (Bruce et al., 2007) and would explain the lower foliar injury after medium-term recovery period for most of the investigated species. Especially *F. excelsior* and *C. monogyna*



recovered very well after a recovery period of nine months. Nevertheless, the previously flooded individuals of *F. excelsior* showed a higher leaf loss compared to the previously unflooded individuals, which is in accordance with the flooding experiment of Frye & Grosse, (1992), where flooded *F. excelsior* saplings showed a reduced aboveground biomass compared to unflooded individuals the following year. This reaction might be an adaptive strategy by reducing energy consumption (Pires et al., 2018). New leaves only sprout when environmental conditions become better (Mommer & Visser, 2005; Pires et al., 2018). The fast recovery of *F. excelsior* and *C. monogyna* was also observed after the first flooding in the previous year and confirms that poor performance during flooding does not necessarily indicate a reduced flooding tolerance, as some species can save energy for later recovery (Schindler et al., 2020; Striker, 2012).

The development of plants after nine months recovery can not only improve, but also deteriorate for some species and lead to even greater damage (Striker, 2012). For example, *S. nigra* showed a low short-term injury, but a high medium-term injury after the first flooding (Schindler et al., 2020). After the new flooding of nine weeks, there was a high short- and medium-term foliar injury. Flood damage effects may persist for up to three years and the time between floods, may result in an additional weakening for some species. This could also explain the lower  $\Delta$  stem diameter of the previously flooded individuals of *C. sanguinea* compared to the previously unflooded ones. A second flooding without a sufficiently long recovery period especially during the early sapling stages could lead to even greater damage (Striker, 2012). Therefore, a longer recovery period before the second flooding could have contributed positively especially to the less flooding tolerant species.

Another example for the potential of stress memories in plants becomes apparent in the study of Ferreira et al. (2007), where they determined the influence of flooding tolerance on seedlings from a floodplain versus upland population of the same species (*Himatanthus sucuuba*). They found out that the floodplain population was more tolerant to flooding in terms of a higher germination rate, survival and growth rate than the upland population. Therefore, there is evidence that such memories can be passed down to offspring to increase their success. We collected most of the seeds in the former floodplain where these effects may not have occurred but it would be interesting to repeat the experiment with seeds from the active versus the former floodplain.

## Conclusion

Contrary to our expectations, a previous flooding, regardless of its duration showed no increased flooding tolerance of the saplings. Therefore, no stress memory towards flooding stress could be observed for our investigated species. The predominant strategy here seems to be recovery after flooding. Therefore, recurring floods without an adequately long recovery period could pose problems for the establishment of saplings in floodplains, especially under changing climatic conditions with increasingly unpredictable and extreme flooding events (Mosner et al., 2015). Due to the complexity of interacting processes, the knowledge about flooding tolerance especially in terms of stress memory and stress recovery needs further investigation.

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# Appendix Chapter 4

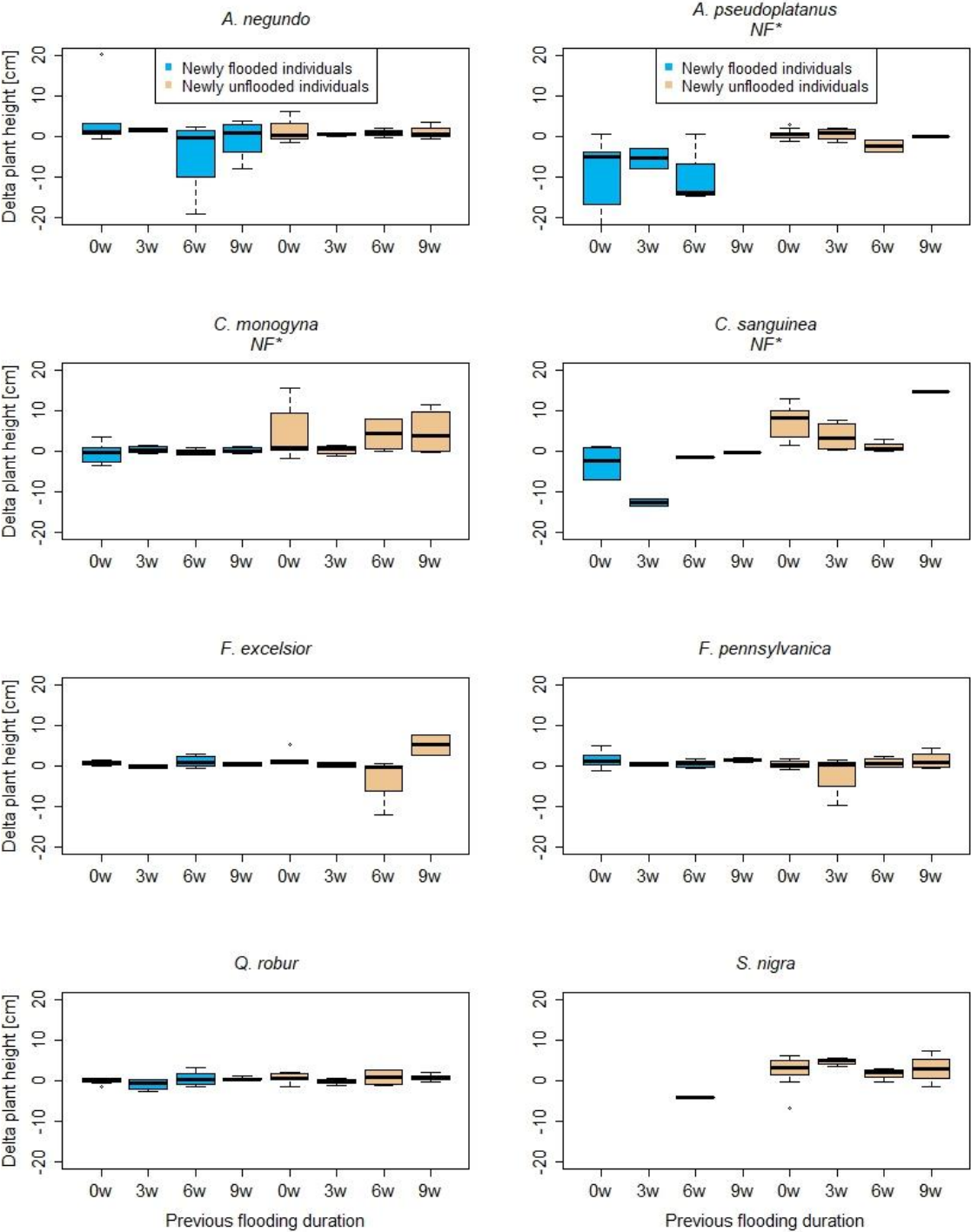


Fig. A4.1  $\Delta$  Plant height of each species depending on the previous flooding duration after a short-term recovery of three weeks; w = weeks; Significant differences between the main effects were marked with capital letters (PF\* - previous flooding, FD\* - previous flooding duration, NF\* - new flooding treatment).



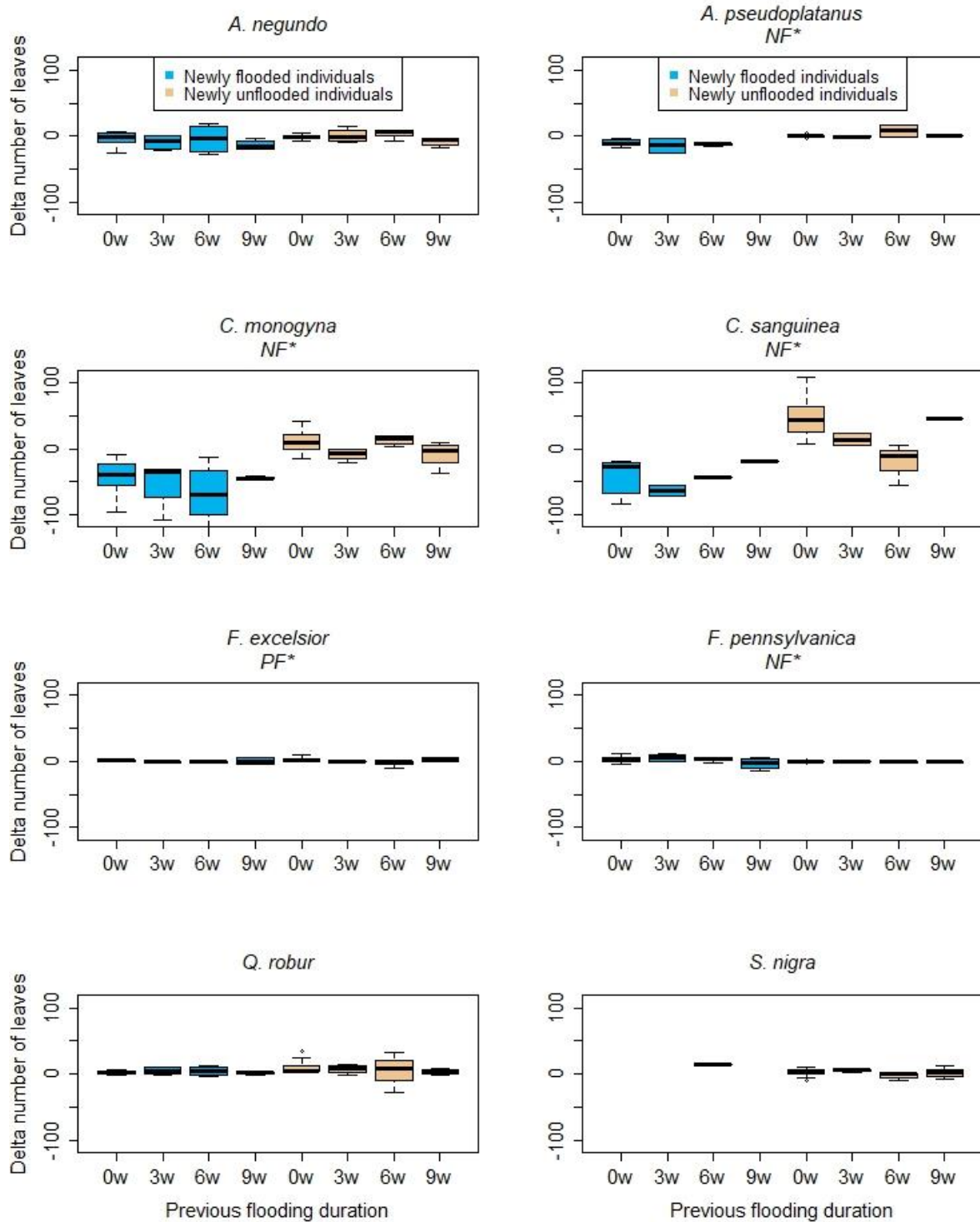


Fig. A4.2  $\Delta$  Number of leaves of each species depending on the previous flooding duration after a short-term recovery of three weeks; w = weeks; Significant differences between the main effects were marked with capital letters (PF\* - previous flooding, FD\* - previous flooding duration, NF\* - new flooding treatment).

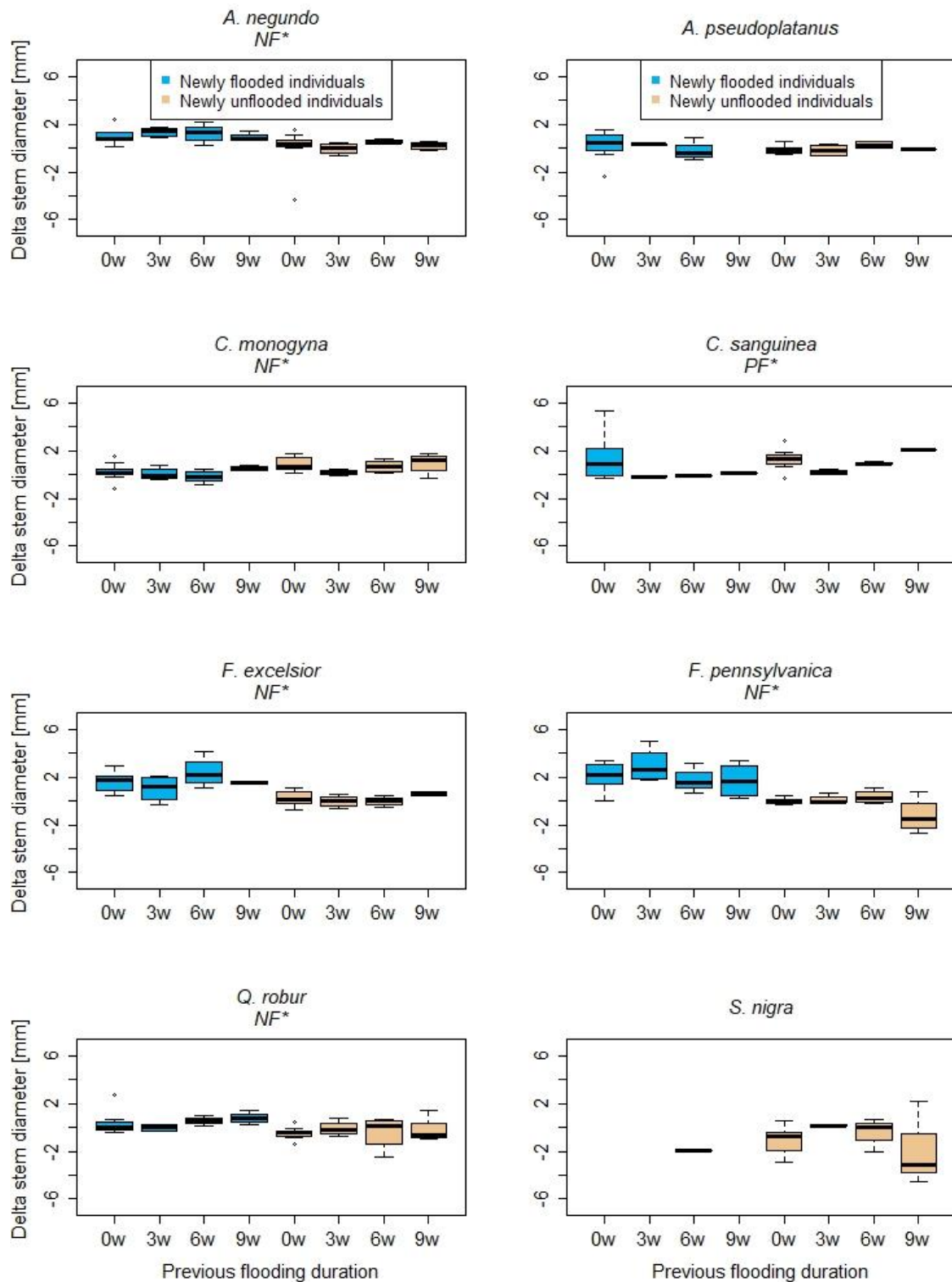


Fig. A4.3  $\Delta$  Stem diameter of each species depending on the previous flooding duration after a short-term recovery of three weeks; w = weeks; Significant differences between the main effects were marked with capital letters (PF\* - previous flooding, FD\* - previous flooding duration, NF\* - new flooding treatment).

## Abstract

Hardwood floodplain forests are among the most structure- and species-rich ecosystems in Central Europe. Due to anthropogenic changes, they have been drastically reduced and belong nowadays to the most endangered ecosystems. Therefore, the restoration of floodplain forests is a central goal of alluvial restoration projects, but at the same time a difficult task due to the complex environmental conditions. Since flooding tolerance can be regarded as key factor for successful establishment of plant species in floodplains, this thesis deals with flooding tolerance of different hardwood floodplain forest species. Further, this thesis combines experimental studies under controlled hydrological conditions with field experiments. The latter were conducted in one of the largest alluvial restoration areas in Germany – the dike relocation area “Lenzen-Wustrow”.

In general, the results of my thesis showed that an increasing flooding duration negatively affects plant performance. Further, after second flooding in the following year, similar flooding tolerance patterns were observed. However, most species were able to recover better after the second flooding compared to the first one, probably also because the individuals were one year older at this point. Nevertheless, a previous flooding experience, regardless of its duration, showed no changes in the flooding tolerance of the saplings, indicating that there is no flooding stress memory in the investigated species. Furthermore, I revealed that for the classification of flooding tolerance, it is highly important to include a recovery period. By this, misjudgments of flooding tolerance patterns of species can be avoided, as plants can either recover after flooding or suffer even more. In general, the species-specific differences in flooding tolerance could be explained by their ability to react to the resulting flooding stress by using morphological, physiological and metabolic adaptations. Species that are able to quickly generate different structures in a large number will cope better even with long periods of flooding.

Although the assessment of the flooding tolerance of different species depending on flooding duration is useful in the context of restoration planning processes, it must be considered with caution as the incorporate variations in site conditions, hydrological parameters and ecological requirements are not included. The field study showed that processes in floodplains are highly dynamic and that long flooding as well as long drought periods must be considered as separate extreme events. Both are unfavorable during early establishment, even though, the mean annual number of flooding days was within the typical growth range of the hardwood floodplain forest

zone. Further, under field conditions, additionally to the hydrological regime, many other factors can influence the establishment of trees, such as herbivory, which caused a high mortality in the study area. As comparable studies in restored floodplains do not exist until now and I could demonstrate how necessary long-term study periods are, it is important that more studies and assessments of establishment success are carried out in the field, covering longer study periods and also take into account the interaction of the various influencing factors more precisely. Only then, it will be possible to provide better predictions and possible solutions for future restoration measures.

## Zusammenfassung

Hartholz-Auenwälder gehören zu den struktur- und artenreichsten Ökosystemen Mitteleuropas. Aufgrund anthropogener Veränderungen wurden sie in der Vergangenheit stark dezimiert, sodass sie heutzutage zu den am stärksten bedrohten Ökosystemen Mitteleuropas gehören. Die Renaturierung von Auenwäldern ist demnach eines der zentralen Ziele von Auen-Renaturierungsprojekten. Gleichzeitig stellt sie aufgrund der komplexen Interaktion verschiedener Einflussfaktoren eine große Herausforderung dar. Da die Überflutungstoleranz als Schlüsselfaktor für die erfolgreiche Ansiedlung von Pflanzenarten in Auen angesehen werden kann, welche für viele Hartholz-Auengehölze allerdings noch unzureichend erforscht ist, zielt diese Dissertation darauf ab, die Überflutungstoleranz verschiedener Hartholz-Auenwaldarten genauer zu untersuchen. Dabei wurden experimentelle Studien mit kontrollierten hydrologischen Bedingungen mit Freilandversuchen in einem der größten Auenrenaturierungsgebiete Deutschlands – der Deichrückverlegung in Lenzen-Wustrow – kombiniert, um den Erfolg zukünftiger Renaturierungsprojekte besser abschätzen zu können.

Es wurde gezeigt, dass eine zunehmende Überflutungsdauer die Entwicklung der Jungpflanzen verschiedener Hartholz-Auenwaldarten stark negativ beeinflusst. Ähnliche artspezifische Überflutungstoleranzen wurden auch im Folgejahr nach einer weiteren Überflutung festgestellt. Allerdings konnten sich die meisten Arten nach dem zweiten Überflutungsexperiment im Vergleich zum Vorherigen des Vorjahres besser von den Überflutungsschäden erholen. Dies lässt sich allerdings auch darauf zurückführen, dass die Individuen bereits ein Jahr älter sind. Weiterhin zeigte ein bereits zuvor erlebtes Überflutungsereignis, unabhängig von deren Dauer, keine Veränderungen der Überflutungstoleranz der Jungpflanzen, was darauf schließen lässt, dass die untersuchten Arten kein Stressgedächtnis hinsichtlich Überflutung ausbilden können. Es wurde ebenso deutlich, dass die Überflutungstoleranz erst nach einer gewissen Erholungsphase eingeschätzt werden sollte, um Fehleinschätzungen zu vermeiden, da sich die Pflanzen nach der Überflutung entweder von den Überflutungsschäden erholen, oder noch stärker leiden können. Die artspezifischen Unterschiede der Überflutungstoleranz werden damit erklärt, auf den Überflutungsstress mit entsprechenden morphologischen, physiologischen und metabolischen Anpassungen reagieren zu können. Diejenigen Arten, die in der Lage sind, besonders schnell verschiedene morphologische Strukturen in hoher Anzahl ausbilden, werden auch mit längeren Überflutungsdauern besser zurechtkommen.

Obwohl das Wissen der Überflutungstoleranzen verschiedener Arten in Abhängigkeit von der Überflutungsdauer, welche unter kontrollierten Bedingungen erfasst wurden, im Rahmen von Renaturierungsprojekten nützlich ist, muss es mit dem Hintergrund betrachtet werden, dass die interagierenden Variationen der Standortbedingungen, die hydrologischen Parameter sowie die ökologischen Anforderungen, die unter natürlichen Bedingungen auftreten, hier nicht berücksichtigt wurden. Die beiden Freilandversuche zeigen wie dynamisch die Prozesse in Auen sein können und wie wichtig längere Untersuchungszeiträume und Erfolgskontrollen sind. Obwohl die mittlere jährliche Anzahl an Überflutungstagen im typischen Wuchsbereich der für Hartholz-Auenwaldarten typischen Bereiche lag, müssen über längere Zeit dauernde Überflutungs- sowie Trockenperioden als Extremereignisse bewertet werden, welche für die frühe Etablierung von Hartholz-Auenwaldarten hinderlich sein können. Darüber hinaus können unter Freilandbedingungen neben den hydrologischen Bedingungen viele weitere Faktoren Einflüsse auf die Etablierung und Naturverjüngung von Bäumen haben, wie beispielsweise der Wildverbiss, der im Untersuchungsgebiet eine große Rolle zu spielen scheint. Aufgrund des Fehlens vergleichbarer Studien in Renaturierungsgebieten und der Notwendigkeit längere Untersuchungszeiträume abzubilden, müssen zukünftige Feldversuche und Erfolgskontrollen, am besten über mehrere Jahrzehnte sowie unter Einbeziehung der Interaktion verschiedener Einflussfaktoren genauer untersucht werden. Nur dann wird es möglich sein bessere Vorhersagen und Lösungsansätze für zukünftige Renaturierungsmaßnahmen entwickeln zu können.

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## 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-University Giessen zur Sicherung guter wissenschaftlicher Praxis” in carrying out the investigations described in this dissertation.

Berlin, 08. May 2021

Melanie Schindler