Philipps Universität Marburg

Habitat distribution and population genetics of riparian *Salix* species in space and time

–

a restoration framework
for softwood forests
along the Elbe River

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The important thing is not to stop questioning.

Albert Einstein

Für Lisa, Melli, Volker und Matti

List of papers

This thesis is based on the following publications and manuscripts, which are referred to in the text by the term “paper” and their Roman numerals.

I. **E. Mosner**, S. Schneider, B. Lehmann, I. Leyer (2011) Hydrological prerequisites for optimum habitats of riparian *Salix* communities – identifying suitable reforestations sites. *Applied Vegetation Science 14(3)*, 367 – 377.

II. A. Radtke, **E. Mosner**, I. Leyer (2012) Vegetative reproduction capacities of floodplain willows – cutting response to competition and biomass loss. *Plant Biology 14(2)*, 257 – 264.

III. I. Leyer, **E. Mosner**, B. Lehmann (2012) Managing floodplain forest restoration in European river landscapes combining ecological and flood protection issues. *Ecological Applications 22*, 240-249.

IV. **E. Mosner**, T. Conradt, F. Hattermann, I. Leyer (manuscript) Azonal vegetation under climate change: Riparian forest responses to climate-driven hydrological changes.

V. **E. Mosner**, S. Liepelt, B. Ziegenhagen, I. Leyer (under review) Floodplain willows in fragmented river landscapes: Understanding spatio-temporal genetic patterns as a basis for restoration plantings.

For **paper I**, I developed together with I. Leyer the concept of the study. I conducted all the field work, partly prepared the hydrological data, performed the analyses and was responsible for the writing. The co-authors contributed with invaluable ideas for the data analyses and comments on the manuscript. For **paper II,** I provided in collaboration with I. Leyer the conceptual ideas, gave support in working out the study design, assisted in data analyses and commented the manuscript. Regarding **paper III**, I was responsible for data collection and analyses for the ecological compartment of the study, contributed parts of the manuscript as well as comments to the whole manuscript. In terms of **paper IV**, I created together with I. Leyer the concept, worked out the study design, prepared vegetation as well as hydrological data for the projections, calculated vegetation projections, analysed the data and mainly wrote the manuscript. Projections of discharge data were provided by T. Conradt and F. Hattermann. All co-authors gave helpful suggestions for the manuscript. For **paper V**, I developed the concept and the study design in collaboration with I. Leyer and B. Ziegenhagen, conducted most of the genetic analyses as well as all data analyses and had responsibility for writing the manuscript. All co-authors provided valuable support regarding data analyses, contributed to result evaluation and commented on the manuscript.

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Summary

Riparian softwood forests belong to the most endangered vegetation types in Central Europe due to diverse river management measures such as dyking or river training. As unmodified hydro-geomorphic processes along rivers are widely lacking, which are necessary to create competition-free establishment sites, natural regeneration of the respective species is almost absent. Hence, restoration measures such as plantings are required but are often declined as it is assumed that plantings lead to an increased flooding risk due to hydraulic effects on water levels. Consequently, restoration of riparian softwood forests is a challenging task given the different interests of economy, society, and nature conservation.

My thesis was conducted within the framework of a project to develop a concept for the establishment of riparian softwood forests combining ecological and flood protection issues along the Middle Elbe River. Main aims of my work were to investigate ecological as well as population genetic aspects of riparian softwood forest species to deliver a basis for improving the success of restoration measures such as plantings. My thesis comprises a total of five studies dealing with different aspects of riparian softwood forest restoration.

In the first study the ecological relationships of distribution patterns of riparian softwood forests and hydrological variables were examined. Therefore, habitat distribution models were developed for two vegetation types, shrubs (Salicetum triandro-viminalis) and trees (Salicetum albae), as well as two age classes, young and old vegetation. They revealed that hydrological variables are significantly related to and substantially determine species distribution, though differences were observed for the different vegetation types as well as age classes. Spatial quantification showed that there is considerable amount of suitable habitat regarding hydrological conditions suggesting that restoration of riparian softwood forest species should be possible from an ecological point of view. Based on the observed ecological patterns advices are given for the selection of suitable planting sites.

Besides abiotic factors, biotic interactions are important determinants for a successful establishment of species. In terms of riparian softwood forest species, competition is known to negatively affect the sexual regeneration. Hence, it could also compromise the success of plantings. In an experimental approach, potential effects of competition and biomass loss on the regeneration capability of vegetative propagules, i.e. cuttings, of diverse riparian *Salix* species were tested. It revealed that also cuttings are prone to competition mainly due to demands for light, indicating that it should be eliminated during establishment phases to increase the success of planting measures. The additionally tested resprouting ability of the species - newly grown biomass was removed after a certain time - disclosed vigorous growth capacities of all investigated floodplain species. This suggests that cuttings should tolerate natural disturbances such as flooding, sedimentation and ice shear to a certain extent. Summarised, cuttings of riparian softwood species should be more suitable for restoration plantings than seedlings.

Overall, results of the first two studies point to a well-defined potential for successful reforestation measures if species requirements regarding abiotic as well as biotic conditions are considered. However, since much debate on such plantings exists the third study was conducted to assess the effect of riparian softwood forest plantings on flooding risk combining habitat distribution models as well as a two-dimensional hydraulic-numerical model. With this approach we could demonstrate that it is possible to identify sites which meet the criteria of both ecological as well as hydraulic suitability. Although hydraulic suitability is a matter of the specific spatial context of selected sites, substantial potential for “safe” plantings can be expected in managed river-floodplain systems. Nevertheless, other measures such as dyke relocation or floodplain excavation, which might be even more suitable to regenerate riparian softwood forests simultaneously reducing flood risk, are discussed.

In contrast to current conditions still disclosing large potential for softwood forest restoration, habitat projections based on climate change induced hydrological alterations point to a further loss of suitable habitat in the future. These were calculated on the basis of the habitat modelling approach in combination with projections of discharges, produced by a hydrological model. Reductions in habitat area are caused by decreasing average discharges leading to lowered water levels on the one hand and little availability of low elevation sites such as depressions or oxbow lakes in the floodplain on the other. Regarding the selection of suitable planting sites for the future, large uncertainty in habitat availability exists due to substantial variability in hydrological projections. However, this uncertainty should be implemented into restoration management to preserve riparian softwood forests in the long term.

While current natural population structures and dynamics of riparian softwood forest species warn about an extremely critical condition regarding the long-term persistence of these vegetation types, results of the genetic population analysis are less alarming. The genetic investigations were conducted to assess the population genetic structure regarding clonal patterns and genetic diversity of the existing stands as basis for the selection of suitable planting material. *Salix viminalis* was used as a model species. Though clonal structures were prevalent no dominance of single clones was detected. Levels of genetic diversity were generally high and no negative effects of floodplain or stand fragmentation on diversity levels were found. Hence, ecological pressures resulting from restricted regeneration potential are far more challenging than possible effects of stand and floodplain fragmentation on genetic diversity levels of riparian softwood forest species. From the observed genetic patterns, advices for the selection of planting material were deduced.

Overall, the results presented in this thesis deliver a sound basis for the restoration of riparian softwood forests based on reforestation. Given the restricted sustainability of these measures additionally other restoration approaches should be considered enabling the "re-dynamisation" of the floodplain and hence the self-preservation of riparian softwood forests.

German Summary - Zusammenfassung

Weichholzauenwälder zählen zu den am stärksten bedrohten Vegetationstypen in Mitteleuropa, bedingt durch Maßnahmen zur Flussbewirtschaftung wie Eindeichungen oder Flussbau. An den meisten Flüssen fehlen unveränderte, hydrogeomorphologische Prozesse weitestgehend, welche notwendig sind, um konkurrenzfreie Etablierungsstandorte zu schaffen. Somit ist eine natürliche Regeneration der Weichholzauenarten kaum noch zu beobachten und Renaturierungsmaßnahmen wie zum Beispiel Pflanzungen sind nötig. Diese werden aber häufig abgelehnt, da angenommen wird, dass diese zu einer Verschärfung des Hochwasserrisikos durch hydraulische Effekte auf die Wasserstände führen. Folglich stellt die Renaturierung von Weichholzauen eine große Herausforderung vor dem Hintergrund unterschiedlicher Nutzungsinteressen von Wirtschaft, Gesellschaft und Naturschutz dar.

Ich habe meine Doktorarbeit im Kontext eines Projektes erstellt, das die Entwicklung eines Konzepts zur Wiederansiedlung von Weichholzauen an der Mittleren Elbe unter Berücksichtigung ökologischer und hochwasserschutztechnischer Belange zum Ziel hatte. Im Rahmen verschiedener Untersuchungen habe ich mich im Wesentlichen ökologischen sowie populationsgenetischen Aspekten verschiedener Weichholzauenarten gewidmet. Die Ergebnisse stellen eine wissenschaftliche Grundlage für Pflanzungsmaßnahmen dar, um deren Erfolg zu verbessern. Meine Doktorarbeit beinhaltet fünf Studien, die sich mit verschiedenen Fragestellungen zur Renaturierung von Weichholzauen beschäftigen.

In der ersten Studie wurden die ökologischen Zusammenhänge zwischen den Verbreitungsmustern der Weichholzaue sowie hydrologischen Variablen untersucht. Dafür wurden Habitatmodelle für zwei Vegetationstypen, für Strauchweiden (Salicetum triandro-viminalis) und Baumweiden (Salicetum albae), sowie für zwei unterschiedliche Altersklassen, junge und alte Vegetation, entwickelt. Die Modelle zeigten, dass die hydrologischen Variablen die Habitatverbreitung signifikant und zu großen Teilen erklären. Dennoch konnten Unterschiede zwischen den Vegetationstypen und Altersklassen gefunden werden. Darüber hinaus verdeutlichte eine räumliche Quantifizierung der Habitate, dass sich erhebliche Teile der Aue aus hydrologischer Sicht als Habitat eignen und dass somit die Renaturierung von Weichholzauen aus ökologischer Sicht möglich sein sollte.

Neben den abiotischen Bedingungen sind generell auch biotische Interaktionen wichtige Faktoren für eine erfolgreiche Etablierung von Arten. Im Falle der Weichholzauenarten ist bekannt, dass sich Konkurrenz negativ auf deren sexuelle

Regeneration auswirkt. Somit könnte diese auch den Erfolg von Pflanzungsmaßnahmen einschränken. In einem experimentellen Ansatz wurden mögliche Effekte von Konkurrenz und Biomasseverlust auf die Regenerationsfähigkeit von vegetativen Reisern bzw. Stecklingen verschiedener *Salix*-Arten getestet (Kapitel 3). Es zeigte sich, dass auch Stecklinge anfällig für Konkurrenz sind und zwar vor allem hinsichtlich der Konkurrenz um Licht. Dies weist darauf hin, dass Konkurrenz während der Etablierungsphase von gepflanzten Stecklingen möglichst vermieden werden sollte, um den Erfolg von Pflanzungsmaßnahmen zu erhöhen. Zusätzlich wurde die Wiederaustriebsfähigkeit der Arten getestet, indem die neu gewachsene Biomasse nach einiger Zeit entfernt wurde. Enorme Wachstumskapazitäten aller untersuchten Auenarten konnten daraufhin festgestellt werden. Daraus lässt sich folgern, dass Stecklinge natürliche Störungen wie Überflutung, Sedimentation und Eisschur vermutlich bis zu einem gewissen Grad tolerieren können. Insgesamt deuten die Ergebnisse darauf hin, dass Stecklinge für Pflanzungsmaßnahmen besser geeignet sind als Sämlinge.

Die Ergebnisse der ersten beiden Studien zeigen ein klar beschreibbares Potenzial für erfolgreiche Pflanzungsmaßnahmen, wenn die Bedürfnisse der Arten bezüglich abiotischer und biotischer Randbedingungen berücksichtigt werden. Da jedoch viel Diskussion um solche Pflanzungsmaßnahmen besteht, wurde die dritte Studie durchgeführt, um die Effekte von Weichholzauenpflanzungen auf das Hochwasserrisiko zu überprüfen. Hierfür wurden Habitatmodelle mit einem zweidimensionalen hydraulisch-numerischen Modell kombiniert. Mittels dieses Ansatzes konnten wir zeigen, dass es möglich ist, Standorte zu identifizieren, die sowohl den Kriterien zur ökologischen als auch zur hydraulischen Eignung entsprechen. Obwohl die hydraulische Eignung eine Frage des spezifischen räumlichen Kontexts der ausgewählten Renaturierungsstandorte ist, kann ein bedeutendes Potenzial für „sichere“ Pflanzungen in wirtschaftlich genutzten Flussauensystemen erwartet werden. Dennoch könnten andere Maßnahmen wie Rückdeichungen oder Abtragungen in der Aue besser geeignet sein, um Weichholzauen zu renaturieren und gleichzeitig das Hochwasserrisiko zu senken. Diese werden diskutiert.

Die jetzigen Umweltbedingungen offenbaren immer noch ein großes Potenzial für die Renaturierung von Weichholzauen. Im Gegensatz dazu zeigen Zukunftsprojektionen von Weichholzauenhabitaten, die auf durch den Klimawandel induzierten hydrologischen Veränderungen beruhen, einen Verlust von geeignetem Habitat. Die Projektionen wurden durch eine Verknüpfung von Habitatmodellen mit Abflussprojektionen berechnet, die Ergebnis eines hydrologischen Modells waren. Die Verminderung von geeignetem Habitat ist einerseits zurückführbar auf geringere Wasserstände als Folge eines verminderten mittleren

Abflusses und andererseits auf die bereits jetzt geringe Verfügbarkeit von niedrig liegenden Standorten in der Aue wie Flutmulden oder Altarme. Hinsichtlich der Auswahl zukünftiger Pflanzungsstandorte existiert eine große Unsicherheit bezüglich der Habitatverfügbarkeit, die durch die große Variabilität der Projektionen der hydrologischen Bedingungen entsteht. Dennoch sollte diese Unsicherheit für Renaturierungsmaßnahmen berücksichtigt werden, um Weichholzauen auch in Zukunft zu erhalten.

Die gegenwärtigen natürlichen Populationsstrukturen und –dynamiken der Weichholzauenarten weisen auf einen extrem kritischen Zustand hin, der die Langzeitpersistenz dieses Vegetationstypus in Frage stellt. Hingegen sind die Ergebnisse der genetischen Populationsanalyse weniger alarmierend. Die genetischen Untersuchungen wurden durchgeführt, um die populationsgenetische Struktur hinsichtlich klonaler Muster sowie genetischer Diversität der existierenden Bestände zu untersuchen. Hierfür wurde *Salix viminalis* als Modellart untersucht. Obwohl klonale Strukturen verbreitet auftraten, war keine Dominanz einzelner Klone festzustellen. Die genetische Diversität der Bestände war prinzipiell hoch und keine negativen Effekte der Auen- oder Bestandsfragmentierung hierauf waren erkennbar. Somit sind ökologische Belastungen, wie sie durch das eingeschränkte natürliche Regenerationspotenzial der Arten entstehen, als wesentlich größere Herausforderung anzusehen im Vergleich zu möglichen Fragmentierungseffekten auf die genetische Diversität der Weichholzauenarten. Aus den beobachteten genetischen Mustern lassen sich dennoch Ratschläge für die Auswahl von Pflanzungsmaterial ableiten.

Insgesamt liefern die in dieser Arbeit präsentierten Ergebnisse eine solide Grundlage für Renaturierungsmaßnahmen von Weichholzauen auf der Basis von Pflanzungen. Da jedoch die Nachhaltigkeit solcher Maßnahmen sehr eingeschränkt ist, sollten ergänzend andere Maßnahmen zur Redynamisierung der Auen in Betracht gezogen werden, um dauerhaft den Selbsterhalt von Weichholzauen zu ermöglichen.

Chapter 1 – Introduction

1. River floodplains in Europe – setting the scene

While river floodplains have a great biological value, they simultaneously belong to the most endangered ecosystems all over the world (Naiman & Decamps 1997, Tockner & Stanford 2002, Jensen *et al.* 2006). Owing to their highly dynamic character caused by the flow regime, riparian floodplain landscapes exhibit much spatial and temporal heterogeneity (Ward *et al.* 1999, Ward & Tockner 2001). Hydrogeomorphologic processes such as erosion and sedimentation featured by sequences of high and low flows create a mosaic of distinct habitat patches differing in environmental conditions such as inundation duration, soil types, etc. (Hughes 1997, Bendix & Hupp 2000, Steiger *et al.* 2003, Francis 2006). As a result, a great variety of vegetation types is promoted with species all differently adapted to the local abiotic conditions of the respective patches. Simultaneously, alternating periods of different flows are also the main drivers of temporal patterns, succession and rejuvenation, likewise enhancing habitat diversity (Ward & Tockner 2001, Baptist *et al.* 2004, Geerling *et al.* 2006, Stromberg *et al.* 2007, Kondolf *et al.* 2007, Nakamura *et al.* 2007). The great variability of processes driven by the hydrologic regime is the basis for high levels of biodiversity (Ward *et al.* 1999, Ward & Tockner 2001). Hence, riparian floodplains range among the most diverse and belong to the most productive ecosystems on earth (Tockner & Stanford 2002).

The role of more or less regularly occurring floods with different magnitudes has long been recognized as the “catalyst” for habitat dynamics and resulting community patterns found in floodplains. Likewise changes in flow dynamics are accountable for structural alterations and hence changes in the composition of floodplain communities (Dynesius & Nilsson 1994, Ward *et al.* 1999, Tockner & Stanford 2002). In Europe, where construction measures date back to the 11th century, most of the rivers lost their natural flow characteristics due to usage by men for navigation and land reclamation (Petts 1989, Tockner *et al.* 2009). The most prevalent river training measures are dams and dykes aiming at water diversion, flood protection, and making land arable (Dynesius & Nilsson 1994, Tockner & Stanford 2002, Gergel *et al.* 2002). Especially dikes have lead to a tremendous loss of floodplain area amounting to about 95 % of the original floodplain area in Europe (Tockner *et al.* 2009). The so-called older floodplain (sometimes also termed fossil floodplain), i.e. the area of the morphological floodplain behind the dikes, is often still influenced by the river water levels (Montenegro & Holfelder 1999, Schwartz *et al.* 2003), resulting for example in inundated areas due to rising groundwater levels in times of river high-water. Nevertheless, hydrological and disturbance conditions greatly differ between the recent (= functional) and the older floodplain which also affects vegetation communities (Gergel *et al.* 2002, Leyer 2004, Leyer 2005). Floodplain fragmentation for instance as a consequence of dyking disrupts hydrochorous dispersal, which is a prevalent characteristic of many typical floodplain species and one important factor for population dynamics as well as genetic diversity of populations (Nilsson *et al.* 2010).

While dyking has caused the loss of almost all floodplain specific processes in the older floodplain, engineering measures such as channelization, dredging, construction of groynes, barrages, navigational locks and dams have led to a deficit of morphodynamics in the recent floodplain, too (Petts 1989, Tockner & Stanford 2002, Buijse *et al.* 2002). As a consequence, natural relocation of the river bed due to erosion and sedimentation is completely prevented and rejuvenation as a starting point for succession only takes place at sites of high shear stress, i.e. along river beds, flooding channels or connected side arms. Moreover, steady aggradation of the floodplain takes place over time as well as river bed incision due to increased flow velocities (Steiger *et al.* 1998, Buijse *et al.* 2002, Baptist *et al.* 2004, Steiger *et al.* 2005). Accordingly, the amount of high elevation sites in relation to the river stage increases, flooding frequencies in the floodplain decrease due to less overbank flooding and groundwater tables in the floodplain drop in response to the lowering of river water levels. This combination of changed morphodynamics and hydrological conditions, which can be summarized as decreased disturbance levels, has fundamental effects on the structure, distribution and dynamics of adapted floodplain communities (Naiman & Decamps 1997, Tockner & Stanford 2002, Lytle & Poff 2004). Especially species of early successional stages, i.e. pioneer species such as riparian softwood forest species, strongly adapted to high disturbance intensities necessary as a starting point to run trough their life cycles, are negatively affected by such changes.

2. Riparian softwood forests – characteristics of an endangered habitat type

One of the most affected vegetation types regarding river regulation are riparian softwood forests. In Central Europe, species structuring this vegetation type comprise mainly

Salicaceae, willows and poplars. Riparian softwood forests together with riparian hardwood forests form the potentially natural vegetation for most parts of the floodplain. Softwood forests are highly adapted to long inundation periods throughout the year (Blom 1999, Glenz *et al.* 2006). At sites where inundation lasts almost throughout the whole vegetation period and especially during spring when seed dispersal of softwood species takes place pioneer annuals and marshland species establish (Blom 1999). At sites of short inundation periods, less adapted hardwood forest species displace softwood species due to competition (Schnitzler 1995, Karrenberg *et al.* 2002). As such, hydrologic conditions such as inundation duration and frequency are among the most crucial environmental factors leading to the vertical zonation of vegetation types in the floodplain (Van Splunder *et al.* 1995, Blom 1999, Van Eck *et al.* 2004, Vreugdenhil *et al.* 2006).

Riparian softwood forests provide important ecological as well as economical functions (Tockner & Stanford 2002, Ward *et al.* 2002, Schnitzler *et al.* 2005). They exhibit high levels of productivity, contribute to water quality maintenance by filtering the water and providing shade, retain sediment and nutrients, stabilise substrate with their large root systems, are valuable for water retention in times of floods and deliver habitat as well as dispersal corridors in a grassland matrix for other species. Nevertheless, riparian softwood forests almost disappeared along most of the regulated rivers in Central Europe due to land transformation by deforestations and changes in flow regime (Hughes *et al.* 2001, Tockner & Stanford 2002, Kondolf *et al.* 2007). Estimations of the UNEP World Conservation Monitoring Program (2000) for continental alluvial forests comprising different *Salix* species as well as *Populus nigra* amount to 99.5 % loss of the natural distribution area. Moreover, only 6 % of current riverine forests (including boreal and Mediterranean alluvial forests) are protected according to the IUCN categories I – IV. In Germany, only 13 % of the recent floodplains are covered by alluvial forests (softwood and hardwood) whereas about one third is used for urban or agricultural purposes and nearly 50 % is used as pastures (BMU & BfN 2009). Moreover, most of the extant softwood forests exist as small stands or woodlands rather than as spacious forests. However, the valuable significance of riparian softwood forests for the functioning of floodplain ecosystems has been recognized (Hughes *et al.* 2001, Ward *et al.* 2002) and is reflected in the listing of this forest type in Annex I of the European Habitats Directive (92/43/EEC 1992) as one of the most endangered habitat types in Europe.

Today, natural regeneration of softwood forests is extremely limited along regulated rivers and woodlands mostly comprise senescent stands (Brown *et al.* 1997, Tockner & Stanford 2002). Two reasons are accountable: continuing land use on the one hand and missing morphodynamics on the other. Land use often occurs across the entire floodplain, from the dykes to the river banks. Since young softwood forest species are prone to grazing (Auble & Scott 1998, Karrenberg *et al.* 2002), successful establishment of seedlings and saplings is mostly suppressed at otherwise suitable sites. However, the probably more limiting factor is missing morphodynamics in regulated rivers.

As typical pioneer species, softwood forest species such as *Populus nigra*, *Salix alba*, *S. x rubens* (the hybrid of *S. alba* and *S. fragilis*), *S. triandra* and *S. viminalis* exhibit life history strategies that make them highly adapted to the specific disturbance conditions of river floodplains. All species produce a vast number of tiny seeds that are primarily anemochorous and secondarily hydrochorous (Karrenberg *et al.* 2002). This allows the species to disperse their seeds across a large floodplain area. Since seed release occurs in early spring and usually coincides with receding water levels after spring floods (Karrenberg *et al.* 2002, Kehl *et al.* 2008), high soil moisture levels - one of the important germination prerequisites - are abundant. However, seedlings of all softwood forest species need open ground without any other vegetation to establish successfully due to their susceptibility to competition by shading (Hughes *et al.* 2001, Karrenberg *et al.* 2002). As a matter of fact, these sites are mostly missing along regulated rivers. Areas where these necessary morphodynamic processes are occurring are mostly confined to locations along the river bank, flooding channels and connected side arms. Here, seedlings and saplings can occasionally be observed. However, as seedlings and saplings are prone to sedimentation, long flooding durations and flood scoring during the first years and at the same time rely on suitable hydrological sequences after germination (so called Recruitment Box Model, Mahoney & Rood 1998), successful establishment is also a rare event at such sites (Hughes *et al.* 2001, Barsoum *et al.* 2004).

3. Restoration of riparian softwood forests – what is the trouble?

Due to the tremendous loss of riparian softwood forests and the considerable fragmentation of extant woodlands, restoration measures to safeguard the persistence of this invaluable vegetation type in Europe are needed. Since the ecological reasons for its decrease and degradation are known and understood, restoration and conservation appears to be a manageable task. However, serious limitations exist.

The regeneration of natural river flow dynamics and especially the re-establishment of morphodynamics is suggested to be the most successful strategy for the restoration of floodplains in general and of riparian floodplain forests in particular (Hughes *et al.* 2001, Tockner & Stanford 2002, Buijse *et al.* 2002, Richards *et al.* 2002, Hughes *et al.* 2005, Beechie *et al.* 2010, Opperman *et al.* 2010). Measures comply with ecologically designed water management strategies and include dam and dyke removal, removal of river bank fixations, reconnection of side arms and meander cut-offs, and excavation of river floodplains (Amoros 2001, Buijse *et al.* 2002, Hughes & Rood 2003, Rood *et al.* 2003, Nilsson *et al.* 2007, Gonzalez *et al.* 2010a). However, floodplain restoration is often constricted to the site scale as economical aspects such as navigation, flood protection or land use hinder reach scale approaches, especially along large rivers (Buijse *et al.* 2002, Hughes *et al.* 2005). Moreover, projects aiming at river reach or even river basin scales need long term planning and the inclusion of many different stakeholders, which appears to be challenging across districts or states within one country and even more so across country borders. The European Water Framework Directive (WFD, 2000/60/EG) might enforce large-scale strategies, as it calls for an integrative river basin management approach across administrative and political borders. However, even with the recognition of the undeniable value of floodplains regarding the protection of water resources (recital 8, 2000/60/EG) and the acknowledged understanding that floodplains are ecosystems which, with regard to their water needs, directly depend on appropriate aquatic systems (article 1a), their protection can only be achieved through measures that are based on aims addressed in article 4 targeting surface water bodies (Korn *et al.* 2005). Moreover, along many large European rivers, the “good ecological status”-target of the WFD might not be accomplishable due to structural and morphological changes as a consequence of river training measures during the last centuries, at least not within the given time frame until 2015, or 2027 for heavily modified water bodies (Hering *et al.* 2010). For example for the Elbe River, it is stated that the good ecological status, including hydro-morphological and physicochemical elements, will most likely not be achieved for 63 % of the water bodies by 2015, whereas only 12 % will most likely achieve this state and for about 25 %

outcomes are unclear (Schulz & Baron 2005). This reflects especially the economical restrictions regarding navigation and flood protection that preclude restoration activities beyond the local scale.

Since most of the riparian floodplain ecosystems in Central Europe are widely degraded restoration measures are necessary to preserve these valuable ecosystems with their highly endangered vegetation types (Tockner & Stanford 2002). However, the successful “re-dynamisation” of most modified river systems seems very unlikely (Jensen *et al.* 2006) and hence a self-adjusting, natural regeneration of riparian softwood forests almost impossible. Thus, “active restoration” (sensu Jensen et *al.* 2006) is necessary where measures include replanting of species to establish the target vegetation types. To be able to effectively set up such restoration measures, knowledge on the species ecology and population structures is a necessary precondition. Moreover, restoration measures should consider potential future changes in the system, for example due to climate change, as well as possible restrictions from an economical point of view to achieve the best possible outcome mastering the different interests in the long term.

This thesis was conducted within the framework of the project “Concept for the restoration of riparian softwood forests along federal waterways as a contribution to ecologically compatible flood protection management” (DBU – AZ 23649) to deliver an ecological basis for reforestation measures of riparian softwood forest species along large regulated German lowland rivers.

Main objectives, as displayed in Figure 1, were to assess the habitat requirements of riparian softwood vegetation types regarding hydrological conditions and to evaluate potential changes in habitat availability in the course of climate change induced hydrological alterations, to assess effects of competition on the establishment success of vegetative propagules of riparian softwood forest species, to rate the potential effects of riparian softwood forest plantings conducted at ecologically suitable sites on flooding levels, and to assess the population genetic structure of a riparian softwood forest species in relation to floodplain fragmentation.

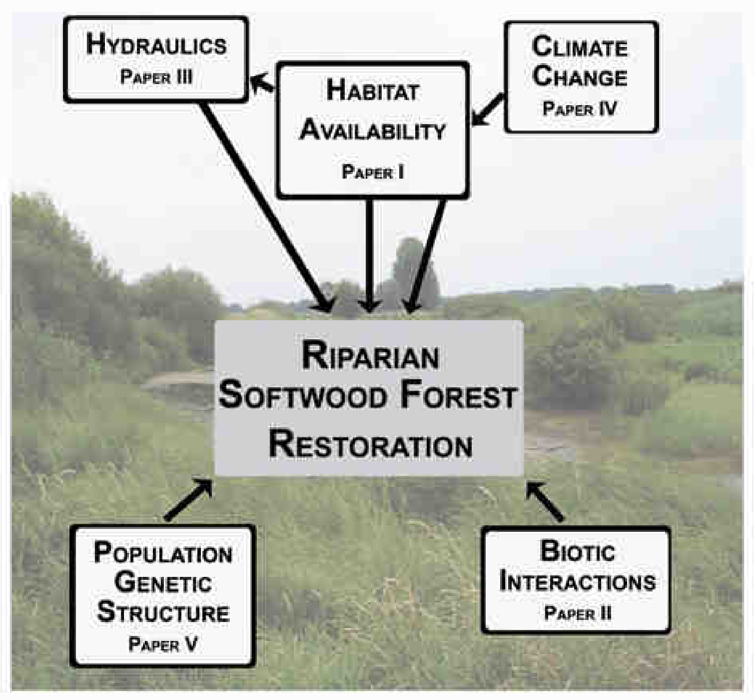

Figure 1: Sketch of the main topics addressed in this thesis.

4. Chapter outline

The following sections will give an overview of important aspects surrounding restoration of riparian softwood forests addressed in the different papers (Fig. 1), which build the main parts of this thesis.

4.1 Chapter 2: Hydrological prerequisites for optimum habitats of riparian *Salix* communities – identifying suitable reforestations sites (Paper I)

In practice, river restoration projects are often carried out at sites mainly chosen because of their availability for such measures. Since site selection often lacks a sound ecological basis regarding species identity reforestation measures often fail (Stanturf *et al.* 2001). Therefore, an ecological understanding of the habitat requirements of target species is necessary to be implemented in reforestation measures to increase the success of plantings.

Paper I presents a modelling study on the habitat distribution of two different riparian softwood vegetation types, shrubs and trees, along a mid-section of the Elbe River. My aim was to investigate the role of different hydrological gradients for the distribution of the softwood vegetation types as well as possible effects of interactions of hydrological factors on their distribution. Moreover, different life stages of softwood vegetation were modelled to reveal differences in habitat distribution in order to identify sites displaying the most suitable habitat for reforestation measures by cuttings. Therefore, I collected presence/absence data of riparian softwood species along a 65 km stretch of the Middle Elbe River. I used habitat distribution models to identify correlations between presence-absence patterns of vegetation types and hydrological factors and to spatially explicitly report habitat distribution of respective vegetation types. The approach of paper I constitutes the methodological basis for further aspects worked out in paper III and IV.

4.2 Chapter 3: Vegetative reproduction capacities of floodplain willows – cutting response to competition and biomass loss (Paper II)

Seedlings of riparian softwood forest species are prone to competition which leads to successful regeneration only at bare ground sites without any competition (Karrenberg *et al.* 2002). However, little is known about conditions necessary for successful establishment of vegetative propagules like branches. Since reforestation measures are mostly based on planting of cuttings, information on the susceptibility of cuttings to growing conditions e.g. competition by surrounding vegetation, is necessary to improve reforestation success.

Paper II presents an experimental approach where in a first experiment three riparian willow species were exposed to different levels of competition by a typical riparian gramineous species under varying soil moisture regimes to test effects on the establishment capability of the willow species. Additionally, resprouting capacity was examined by removing the aboveground biomass to let species resprout a second time. In a second experiment, the growth performance of the same riparian softwood forest species and additionally two fen willow species were tested under differing soil substrate and moisture conditions. Similarly to the first experiment, above- and belowground biomass was completely removed and resprouting ability for the different species was evaluated.

4.3 Chapter 4: Managing floodplain forest restoration in European river landscapes combining ecological and flood protection issues (Paper III)

Besides the aspect that restoration of natural morphodynamics is mostly not feasible along large rivers that are used for navigation purposes (Buijse *et al.* 2002, Hughes *et al.* 2005), severe restrictions to the restoration of riparian softwood forests by plantings apply due to flood protection issues (Hughes *et al.* 2005). Woody vegetation exhibits strong hydraulic effects on flowing water by slowing down flow velocity due to increased surface roughness, leading to an increase in the water level within and upstream of the vegetation structure, the so called backwater effect. Today, most of the river floodplain systems in Central Europe provide extremely restricted inundation areas due to the construction of dykes. Extreme flooding events such as the large Elbe flood in 2002 suggest that any measures potentially increasing inundation levels such as softwood forest plantings could have fatal consequences. Therefore, authorities are very conservative in permitting such measures (Thomas & Nisbet 2007). However, there are no univocal results of the “negative” effects of softwood forest plantings on flooding risk, since this is a matter of the spatial context of the surrounding floodplain as well as the structure and size of plantings.

To improve knowledge and provide a basis for riparian softwood restoration, paper III draws up a conceptual framework for assessing hydraulic effects regarding water level increases of softwood forest plantings based on a combined ecological and hydraulic modelling approach. The approach was developed for a 13 km river stretch in the study area and tested for two different planting scenarios. Habitat distribution modelling (approach paper I) was first conducted to identify suitable reforestation sites. In a second step, hydraulic effects of scenarios with a total planting size of 32 ha and 49 ha were tested based on a 2-dimensional, hydraulic-numerical model (2D-HN) to identify potential sites that do not cause any intolerable increase in water levels.

4.4 Chapter 5: Azonal vegetation under climate change: Riparian forest responses to climate-driven hydrological changes (Paper IV)

In addition to the threats of riparian softwood forests due changes in the river floodplain structure by river regulation and training measures climate change will most likely pose another danger for riparian vegetation. Besides increases in temperature, climate change is expected to change runoff patterns of river catchment areas due to alterations in precipitation patterns (Palmer *et al.* 2009) and this in turn will affect water levels in rivers and flooding conditions in floodplains. So far, impacts of climate change are mostly assessed using large scale modelling approaches to evaluate the effects on species distributions for regions, countries and continents. However, such approaches might be restricted in their potential to express climate change threats on species if their distribution is rather dependent on local conditions than on those at the macro scale as it can be expected for azonal floodplain vegetation.

In paper IV, I assess the possible effects of climate change induced hydrological changes along the Middle Elbe River on the small scale distribution of softwood forest habitats. I applied habitat distribution models for two riparian softwood communities (approach paper I) based on the current status of hydrological conditions as well as for future conditions. For this purpose, I used the results of a semi-distributed eco-hydrological model, i.e. river discharges of 15 out of 100 simulation runs for each of two future periods, 2023-2033 and 2043-2053, to deduce future projections of the hydrological input variables for the distribution models. Intersections of the distribution of current and future habitats for the different vegetation types and additionally life stages were conducted to evaluate potential effects on the extant vegetation as well as relevance for reforestation measures.

4.5 Chapter 6: Floodplain willows in fragmented river landscapes: Understanding spatio-temporal genetic patterns as a basis for restoration plantings (Paper V)

The genetic constitution of populations is a fundamental factor for their persistence since it affects the fitness of present populations as well as the adaptation potential to varying environmental future conditions (Booy *et al.* 2000, Frankham 2005, Pautasso 2009). Where populations of species have undergone fundamental changes due to anthropogenic influences such as habitat loss and habitat fragmentation changes in the genetic constitution of populations can be expected. Thus, conservation and restoration measures directly targeting the recovery of populations should not only focus on the ecological needs of the corresponding species but should also attend to a vital genetic population structure of the focal species.

Paper V is concerned with the genetic population structure of the riparian willow *Salix viminalis*. I investigated potential differences in the genetic constitution of different stand types in different floodplain compartments (recent vs. older floodplain) and of different age classes (old vs. young stands). Aim was to assess the ability of softwood forest species to cope with changed dynamics and habitat loss/fragmentation from a population genetics' point of view. Major aspects of investigations were clonal structures as well as the genetic diversity of stands. Observed patterns were used to deduce recommendations for the selection of suitable planting material for reforestation measures of riparian softwood forests.

Chapters 2-6 have all been submitted to peer-reviewed, international, scientific journals and are either already published or accepted for publication, or are currently under review. They represent closed entities that can be read independently of each other. This structure, however, leads to some redundancy in content among the chapters.

5. Study area - the Elbe River

The Elbe River was chosen as the study area since it belongs to those river systems in Germany, which exhibits fairly unaltered river flow dynamics (i.e. mostly free flowing with only few impoundments) hence having pronounced potential for restoration activities. On the other hand, the Elbe River and its floodplains are also economically used (navigation, agriculture, etc.) causing conflicts between economical and conservation issues thereby restricting restoration capacities from a conservation point of view.

After the Danube and the Rhine River, the Elbe River is the third longest river in Europe with a length of 1.094 km (Tockner *et al.* 2009). It originates in the Giant Mountains in the Czech Republic at an elevation of 1.386 m a.s.l. (IKSE 2005) and discharges into the Northern Sea, crossing the German Federal States Saxony, Saxony-Anhalt, Brandenburg, Mecklenburg-West Pomerania, Lower Saxony and Hamburg. As such, it flows through different topographical regions, from middle mountain ranges to large lowland areas. It can be broadly divided into three different sections, the Upper, Middle and Lower Elbe (IKSE 2005). The Upper Elbe comprises the Czech part of the Elbe River as well as the section to German river km 96 and it is characterized by geomorphological aspects of the surrounding mountainous region. The Middle Elbe includes the lowland sections downstream to the impoundment of Geesthacht, the only weir in the German part. The section downstream of the weir and the estuary build the Lower Elbe, which is characterized by the tidal influence of the Northern Sea.

The Elbe River drains a catchment area of about 148.000 km^2, which equals 64% of the area of the Czech Republic and about 27 % of Germany (DEWA-Europe 2004, Fig. 2). About 25 million people live in the catchment area, which amounts to 58 % of the Czech population and 23 % of the German (DEWA-Europe 2004). Consequently, the Elbe River has important economical values. It is mostly used for obtaining drinking water, as well as water for industrial and irrigation purposes. Moreover, the Elbe River functions as a waterway for navigation. River training to make it navigable has been conducted during the past centuries and until the middle of the 19th century most of the measures were established (Scholten *et al.* 2005). They include shoreline fixation by ripraps and more than 6.900 groynes (vertical structure in relation to the riverbank to interrupt water flow and prevent erosion), meander cut-offs, and the construction of training walls. However, though river training has led to a prevention of lateral movements of the river bed by erosion and sedimentation processes, in the middle section across 489 km the Elbe River is free flowing with a fairly natural flooding regime (Tockner *et al.* 2009).

Another important anthropogenic influence are dykes, which were built for land reclamation. First constructions date back to the 12th century and in the beginning of the 19th century, die dyke line along the Elbe River was closed (Scholten *et al.* 2005), resulting in the fragmentation of the morphological floodplain into the recent, actively inundated floodplain as well as the older floodplain (Fig. 2). Recent assessments of the loss of floodplain area along German rivers estimate along the Elbe River between 50 % and more than 90 % loss, with mostly 80 % to 90 % for the Middle Elbe (BMU & BfN 2009). Besides missing morphodynamics, floodplain fragmentation certainly constitutes the biggest impact on the structure and functioning of the floodplain, including the floodplain ecosystem (Leyer 2005). Moreover, the reduction of the floodplain and therewith inundation area has fatale consequences on the dimension of large flooding events, like the devastating summer flood from 2002 along the Elbe River demonstrated.

The study area comprises a section of the Middle Elbe from river km 410 to km 475 (Fig. 2). It is climatically located in the transition zone between an oceanic and continental climate from the western to the eastern parts, respectively. The annual mean temperature is about 8.5°C and the annual precipitation on average 541 mm (Seehausen, period 1960-1990, Deutscher Wetterdienst). The hydrological regime of the Elbe River can be described as pluvio-nival (rain-snow type) with lowest discharges in late summer (August/September) and highest discharges in early spring (March/April) due to snow melting in the Giant Mountains (IKSE 2005). Thus, flooding usually occurs in spring but can also emerge throughout the other seasons, depending on weather conditions in the catchment area. Discharge varies strongly in the study area (minimum-maximum discharge Wittenberge for the period 1964 – 1995: 195 – 3250 $m^3 * s^{-1}$), resulting in great inter- as well as intra-annual variability (Fig. 3).

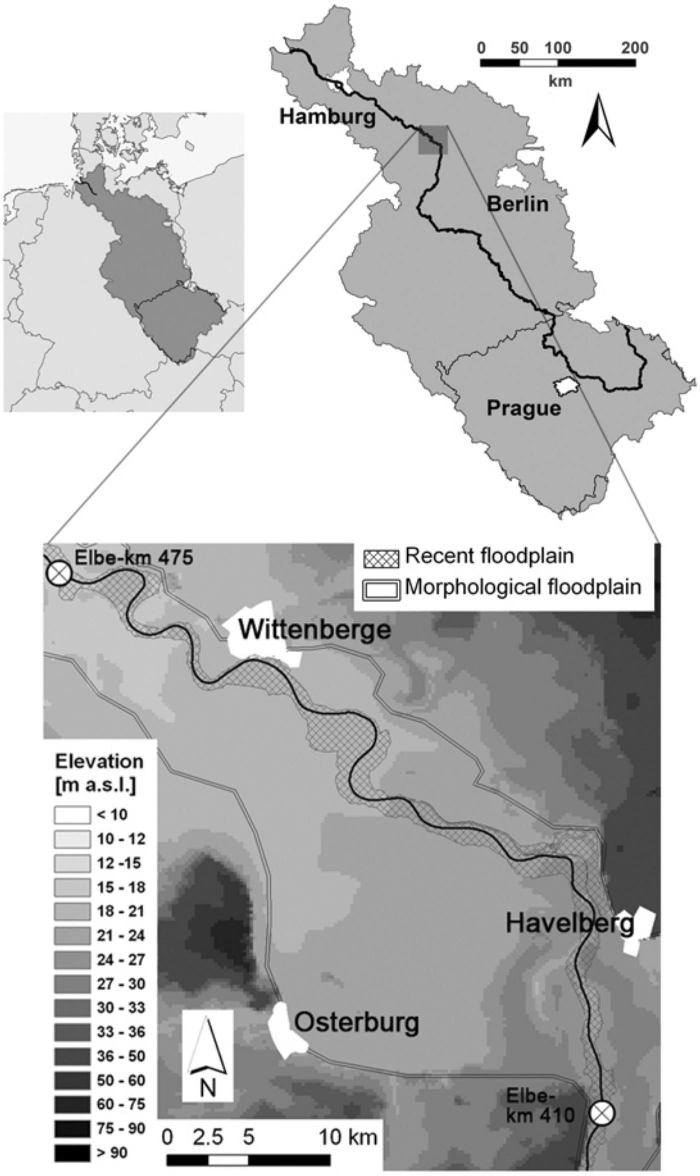

Figure 2: Map of the geographical location of the study area. Upper left: Location of the Elbe catchment in Central Europe. Upper right: Elbe catchment with the location of the study area. Lower: Detailed map of the study area with indication of the recent and morphological floodplain. Indicated river kilometres display the borders of the study area.

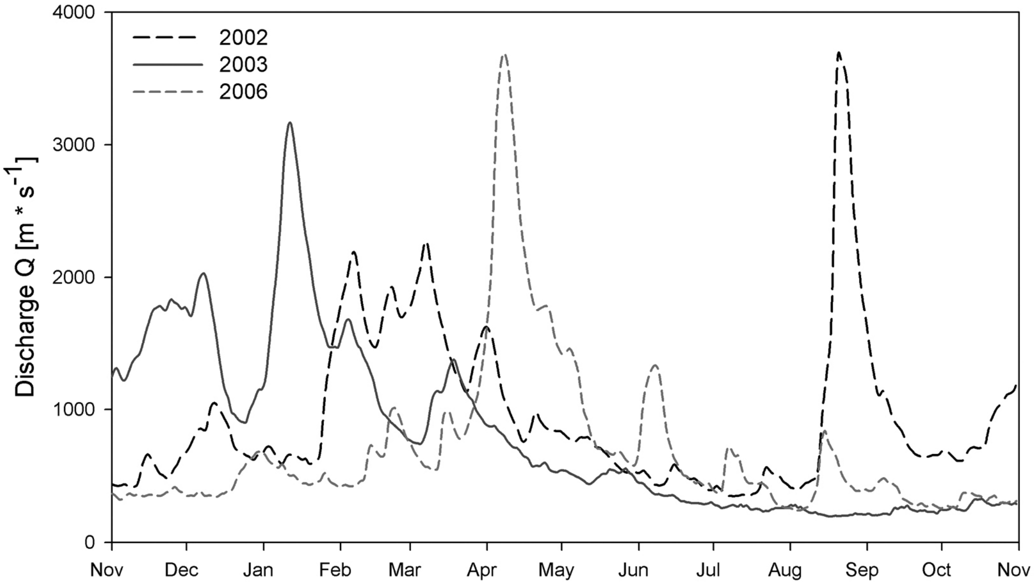

Figure 3: Annual hydrograph of discharges at the river gauge Wittenberge for three different hydrological years (data provided by the Federal Institute of Hydrology [BfG]).

Throughout the study area soils in the floodplain are characterized by a deep layer of gravel, followed by fluvial sands and finally covered by a layer of alluvial clay (= alluvial loam) of varying depth. The different layers are a consequence of geological processes during the Weichselian glaciation forming the Middle Elbe glacial valley and sedimentation processes due to varying water levels during the Holocene (Scholz *et al.* 2004). Especially hydro-morphological processes, i.e. sedimentation and erosion, have led to a strongly textured microrelief of the soil surface in the floodplain.

The groundwater situation in the Elbe river floodplain is strongly influenced by the river water levels (Montenegro & Holfelder 1999), which is ascribable to the highly permeable sediments of the riverbed, the fluvial sands, leading to a strong hydraulic link between the river water and the floodplain aquifer. Usually, during low water periods effluent conditions prevail where groundwater drains into the river. During high water periods the situation is vice versa. The influence of river water levels on the variability of groundwater levels can be observed across large distances of more than 1.5 km away from the river (Fig. 4, Schwartz *et al.* 2003). As a result soil moisture is also influenced by the river stage, which can lead to nearly saturated soils at low lying sites in relation to the river stage compared to fairly dry sites on high elevation sites.

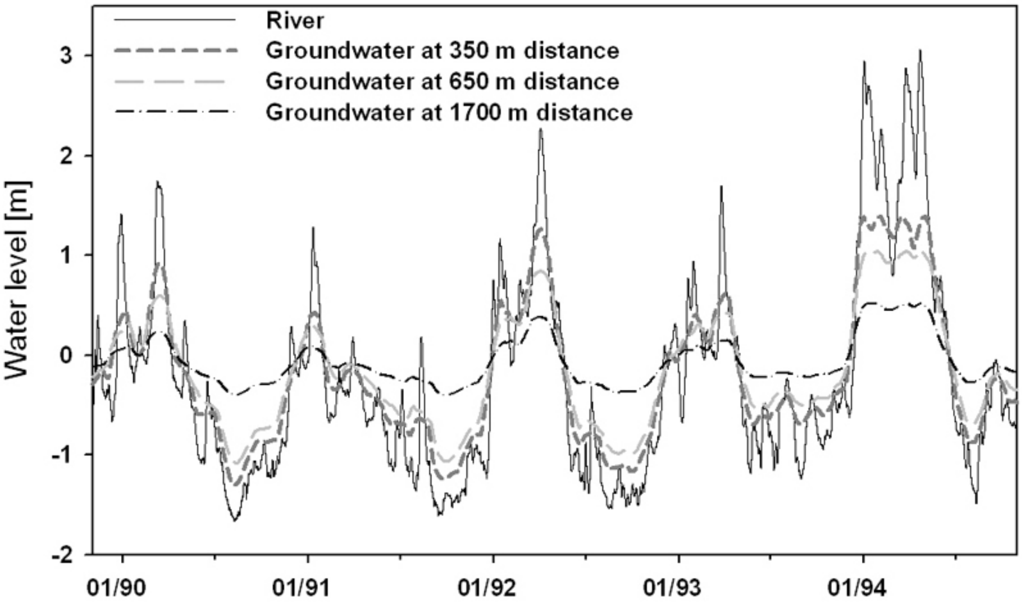

Figure 4: Standardised hydrographs (to zero mean) of water levels of the Elbe River (river gauge Wittenberge) and three groundwater wells, located in different distances in relation to the river, for a 5 year period (data provided by the State Environment Agencies Brandenburg and Saxony-Anhalt and the BfG).

Land use in the floodplain is primarily structured by agriculture. In the recent floodplain, mostly grassland prevails with often more than 50 % of the active floodplain area being used either as pastures or meadows (Fig. 5a, Scholz et *al.* 2004). Though farming is predominantly conducted in the older floodplain, it occurs to a certain extent in the recent floodplain at high elevated sites or locations protected by summer dykes, too (Scholz *et al.* 2004). Forests are mostly confined to the older floodplain, although an old hardwood forest of about 200 ha in size can be found in the most westerly part of the study area. However, riparian softwood forests are usually found as much smaller fragments. The largest continuous softwood woodland in the study area with about 7 ha is located close to the village of Cumlosen (Fig. 5b, 5c).

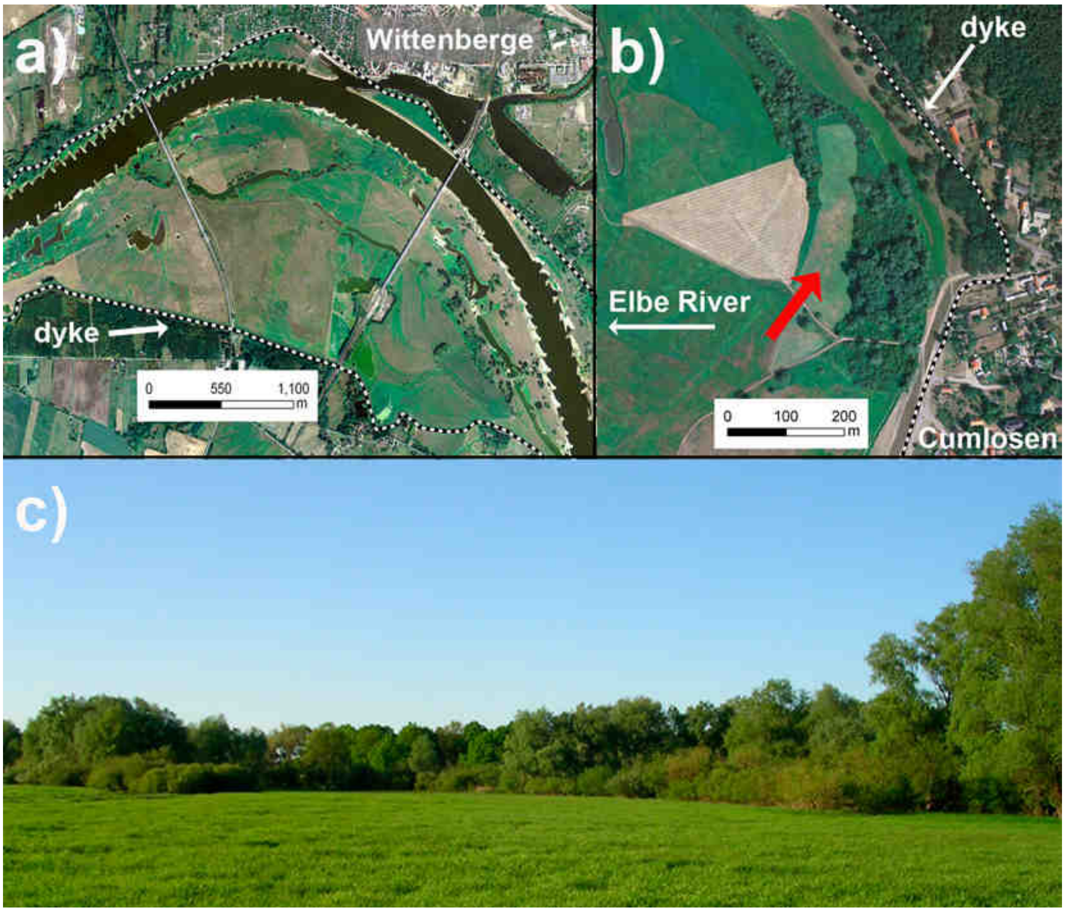

Figure 5: Aspects of the active floodplain in the study area: a) orthoimage of the active floodplain in the vicinity of Wittenberge (© BfG); b) orthoimage of a softwood woodland in the vicinity of Cumlosen (© BfG); the red arrow indicates the line of sight of the photography; c) riparian grassland with riparian softwood woodlands in the background comprising the two vegetation types, the aboreal Salicetum albae with *S. alba* and *S. x rubens* and the shrubby Salicetum triandro-viminalis with *S. triandra* and *S. viminalis.*

Chapter 2

Hydrological prerequisites for optimum habitats of riparian *Salix* communities – identifying suitable reforestations sites

Eva Mosner, Sandra Schneider, Boris Lehmann & Ilona Leyer

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Abstract

Question: What are the hydrological requirements for the successful reforestation of riparian *Salix* communities? Do differences in site conditions between various life stages of woody vegetation types need to be considered? Do interactions between hydrological factors influence distribution patterns?

Location: Mid-reaches of the Elbe River, Germany.

Methods: Young and old life stages of two different riparian *Salix* communities were surveyed in 1067 plots of 400 m^2 to determine hydrological growth conditions using habitat distribution models. Models were extrapolated in a Geographic Information System to quantify the extent of potential stands available for reforestation measures.

Results: Average water level and water level fluctuations were related to different vegetation types as well as to the age classes of the vegetation types. Differences in hydrological niches of young and old vegetation of the two vegetation types (tree community versus shrub community) could be identified. Moreover, the shrub vegetation was influenced by the interaction of average water level and fluctuations. Comparison of the distribution of current vegetation and suitable habitat revealed that considerable areas of the floodplain were suitable for the reforestation of *Salix* woodland communities.

Conclusions: Hydrological variables explain the distribution patterns of riparian *Salix* communities in the active floodplain when different life stages, vegetation types and interaction of variables are included in the analyses. This information can be used to recommend suitable sites for Salix plantings in riparian landscapes.

Introduction

Floodplain woodlands accomplish important economical and ecological functions such as high productivity, structural and species diversity, maintenance of water quality, water retention, sediment and river bank stabilization (Tockner & Stanford 2002; Ward *et al.* 2002; Schnitzler *et al.* 2005). One subgroup of riparian woodlands are the so-called ‘softwood’ forest communities composed of species from the family Salicaceae, which are highly adapted to the hydrological conditions of the riparian system (Scott *et al.* 1996; Blom 1999; Karrenberg *et al.* 2002). While deforestation for agriculture has led to the enormous reduction of riparian softwood woodlands, changed flow regimes and a lack of establishment sites are responsible for the current lack of regeneration and over-aged populations on these floodplains (Brown *et al.* 1997; Tockner & Stanford 2002).

Sexual propagation by seeds is controlled by various factors such as the presence of open sites, sufficient moisture in combination with suitable soil substrates, lack of burial by sedimentation, and no extended flooding during the growing season. Along European lowland rivers, conditions for regeneration are often only met along river banks, floodplain gullies or flooded channels, which are too wet to be used for agriculture. However, establishment of woodlands at these sites is mostly prevented because of river training measures and flood protection issues (Baptist *et al.* 2004). Consequently, riparian softwood woodlands in Europe have experienced a dramatic decline in recent centuries (Brown *et al.* 1997; Harper *et al.* 1997; UNEP-WCMC 2000). These woodlands are considered to be one of the most threatened natural ecosystems and are listed in Annex 1 of the European Habitats Directive.

Restoration of regeneration processes of floodplain woodlands requires the restoration of natural river flow dynamics as well as geomorphological processes. Although there have been attempts to restore the natural dynamics of hydrologic processes in many rivers, such actions are often not feasible, particularly for large European river systems where economic and social interests prevail (Hughes *et al.* 2001; Buijse *et al.* 2002). Nonetheless, current threats affecting endangered floodplain woodlands require prompt action to conserve the natural regeneration potential of existing stands. Without prompt action, the future persistence of floodplain woodlands could be seriously compromised. Planting floodplain woodlands with cuttings/saplings can mitigate further loss and encourage vegetation establishment, and is currently one of the most frequently practiced restoration measure (Stanturf *et al.* 2001).

Suitable hydrological conditions are a fundamental prerequisite for determining the persistence of riparian species in the floodplain. The responses of softwood forest species to flooding and water table levels have been examined in many studies and are generally well-understood (Van Splunder *et al.* 1995; Amlin & Rood 2001; Francis *et al.* 2005; Francis & Gurnell 2006); however, the requirements of different life stages and the effects of interactions between hydrological variables have seldom been addressed and even less so as prerequisites for plantings. For example, woody vegetation is known to change its habitat through sediment deposition so that aggradation of the floodplain occurs over time (Steiger *et al.* 2005; Gurnell & Petts 2006). Hence, it can be assumed, that current sites of old riparian woodlands were once of a different elevation and hydrologic regime (Nakamura *et al.* 2007) and this information would have implications for the identification of suitable planting sites.

Another consideration is the role of interacting abiotic conditions, which is often crucial for the establishment and survival of woody riparian species (Hughes *et al.* 2001; Guilloy-Froget *et al.* 2002). Indeed, there is evidence that interactions between hydrological variables explain a significant part of species occurrences and composition in floodplains (van Coller *et al.* 2000; Leyer 2005). Consequently, floodplain woodland restoration projects are likely to fail if basic hydrological determinants and their main interactions are not included in the selection of restoration sites (Stanturf *et al.* 2001).

In this study, life stages were modelled independently to shed light on the potentially different correlations between young and old individuals of a species and their environment. Interactions between hydrological explanatory factors were also tested to expose less obvious patterns in species distribution.

More specifically, the following questions were addressed: (1) What are the hydrological requirements for successful reforestation of riparian *Salix* communities? (2) Should differences in site conditions between different life stages of different woody vegetation types be considered? (3) Do interactions between hydrological factors influence distribution patterns?

These investigations aim to contribute to a better understanding of the hydrological features governing the distribution of woody riparian species and to help identify the hydrological conditions most suitable for plantings to help improve the restoration success of riparian *Salix* woodlands in Central Europe.

Methods

Study area and species

The Elbe River is one of the largest rivers of Central Europe, originating in the Giant Mountains of the Czech Republic and discharging into the North Sea. It has a catchment area of 148 242 km^2 and a total length of 1094 km (Tockner et al. 2009). The present study was carried out along the mid-reaches of the Elbe River in the vicinity of Wittenberge (52°59′ 41.39′′ N, 11°45′9.56′′ E, river kilometres 415–475) in the active floodplain (i.e. the actively inundated area that is about 0.6 to 5 km wide). This stretch of the river is characterized by an annual discharge of about 715 m^3 * s^{-1}. The highest water levels occur in spring (Mar–May) and the lowest between Aug and Oct (Scholten *et al.* 2005). The flow regime in the study area retains strong, seasonal water level fluctuations (minimum to maximum difference in water level for river gauge Wittenberge for the period 1964–1995 was 5 m) and the floodplain is characterized as active (Tockner *et al.* 2009).

River management has contributed to a substantial narrowing of the floodplain. The construction of dykes dates back to the 12th century with nearly the full extent of the floodplain along the middle and lower reaches of the Elbe River having become channelized by the 19th century. At present, only about 25% of the active floodplain remains (Scholten *et al.* 2005). Furthermore, channelization, creation of cut-offs, dredging and river bank stabilization have led to fundamental changes in the river morphology and hydrological regime of the river and the adjacent floodplain (IKSE 2001).

The floodplain of the study area was formerly covered by riparian softwood and hardwood woodlands, which were cleared for agricultural use and flood protection. Only small patches of softwood woodland remain. These can be divided into two vegetation types: the shrubby vegetation type Salicetum triandro-viminalis Lohm, containing the shrubby species *Salix triandra* L., *Salix viminalis* L. and *Salix purpurea* L., and the arboreal vegetation type, the so-called Salicetum albae Issler, comprising medium-sized to tall trees of *Salix alba* L., *Salix x rubens* Schrank and *Populus nigra* L. In our study, *S. purpurea* and *P. nigra* were not included because these only occurred occasionally and thus could not be modelled.

Vegetation sampling

Species distribution data were gathered during two periods in 2006 and 2007. As only remnant stands of riparian softwood woodlands were left in the study area and these were distributed across a range of environmental gradients, a stratified-randomized sampling design was employed (Hirzel & Guisan 2002). All stands of woody riparian vegetation across the entire vertical and lateral gradient were identified using aerial images. Regular grids with a cell size of 400 m^2 were used to randomly select single cells (=plots) at these sites, comprising a total area of 5% (1067 plots ≈42.7 ha) of the identified stands.

In each plot, the presence/absence of the target species, the dendriform *S. alba* and *S. x rubens* and the shrub-like *S. viminalis* and *S. triandra* was noted. The precise position (deviation<1 m) of one randomly selected individual of each species present within the plot was recorded with a GS20 DGPS with WoRCS Real-Time Beacon System (Leica Geosystems, Munich, Germany). Individuals of each species were further divided into two age classes. As an exact age determination for shrubs or trees was not possible, species were indexed as ‘young’ or ‘old’ depending on indicators of plant age, such as stem diameter and height (Schnitzler 1995). Furthermore, degree and position of branching and evidence of flowering were recorded to classify individuals because field observations showed high correlations to diameter and height. Individual trees of the above-mentioned species were categorized as young when their diameter at breast height was smaller than 30 cm, height smaller than 5 – 6 m, branching occurred below breast height, no evidence of flowering was detectable and the whole habitus resembled a shrub. The classification of shrubs was based on stem diameters with ‘young’ individuals not exceeding 15 cm for the biggest branches, heights of <3 m and very dense branching. Despite a wide range of age cohorts, along the whole river stretch, few seedlings were detectable. Hence, seedling stages could not be investigated.

Hydrology

Hydrological variables as the most influential variables (Gurnell 1997; Bendix & Hupp 2000; Francis & Gurnell 2006) available as spatial information were used to model species habitat distribution. Two vertical gradients and one lateral gradient were included: (1) average water level (AWL), i.e. depth to the water table (with 0=level of top ground surface, negative values=below surface, positive values=above surface); (2) average flood duration; and, (3) the standard deviation of hydrographs (changes in discharge or water levels over time) as a measure for water level fluctuations (WLF).

Both average water level and flood duration were derived from a one-dimensional hydrodynamic-numerical model (Nestmann & Büchele 2002) and a high resolution Digital Elevation Model (DEM). The DEM was created from an airborne laser scanner survey from 2003/2004 with a spatial resolution of 2 m × 2 m. The reference level for the average water level calculations was based on the average discharge (712 $m^3 * s^{-1}$) of the Elbe River. To compute the average water level in the floodplain, the average water level of the river (=reference level) was extrapolated into the floodplain. Thus, average water level as well as flood duration in relation to the floodplain surface could be calculated for each grid cell in the GIS.

Water level fluctuations were calculated based on the relation of river level fluctuations and water level fluctuations within the floodplain (Montenegro & Holfelder 1999; Schwartz *et al.* 2003). Weekly water level data from 11 ground water gauges (seven in front of the dyke and four behind it) from periods between 1989 and 2004 within the study area were transformed into continuous hydrographs. The data were analysed by means of polynomial regression with river water level of the river gauge of Wittenberge as the explanatory variable (Fig. 1). Depending on the distance between the various gauges and the river, fluctuations in water levels of the floodplain are both dampened and delayed in relation to river levels; moving averages and smoothing functions were applied to the hydrograph of the river water level to account for the delays and the diminished fluctuations of the groundwater levels (Crawley 2002). The resulting polynomial function of each ground water level was used to develop continuous hydrographs by simply applying functions on the time-series of the river gauge. Finally, the standard deviation of the water level fluctuations for each time-series was calculated. Subsequently, the standard deviation was tested against distance to the river comparing a linear, a quadratic and an asymptotic model. Best fits were determined using ANOVA's. The best model (asymptotic) was used to interpolate water level fluctuations across the floodplain, from the river to the dyke lines, in a GIS to obtain continuous information about water level fluctuations across the whole floodplain. Interpolation was conducted applying the function Topo to raster in Arcgis 9.3 (ESRI, Redlands, CA, USA).

Further data preparation

For data analyses, presence of the shrubby species *S. viminalis* and *S. triandra* as well as the tree species *S. alba* and *S. x rubens* were combined into the corresponding vegetation types, the Salicetum triandro-viminalis (hereafter referred to as shrubs) and the Salicetum albae (hereafter referred to as trees), respectively as response variables for the modelling approach.

As grazing is known to affect the establishment of willows (Van Splunder *et al.* 1995), 'land use' (not mowed/grazed versus mowed/grazed) was included as an additional predictor. A GIS was used to calculate the total amount of extant softwood woodlands in the study area with all stands larger than 0.2 ha included.

Habitat distribution models

Habitat distribution models were designed to relate the occurrence of softwood forest species to environmental descriptors (Guisan & Zimmermann 2000). Logistic regression (i.e. generalized linear models with logit link and binomial error structure) was applied (Hosmer & Lemeshow 2000), which is a simple method to predict species distribution (Guisan & Zimmermann 2000; Austin 2002). In addition to simplicity, generalized linear models were chosen because of their parametric character, which allows the balancing of data gaps that would otherwise lead to nonsense relations of explanatory variables and species occurrence (Pearce & Ferrier 2000). Before fitting models to the data, predictor variables were first tested for multicollinearity by applying correlation analysis (two-sided Spearman rank-correlation test). Flood duration was excluded from further analyses owing to high collinearity with the average water level (r_s=0.99), where the average water level had more explanatory power than the flood duration when solely tested by univariate analysis (Fielding & Bell 1997). For variable selection, we applied stepwise backwards selection with an exclusion criterion of *P*<0.05. Model selection was based on the likelihood ratio test (Hosmer & Lemeshow 2000). In addition to linear terms, quadratic terms for the average water level were included because unimodal responses over long gradients occurred. However, water level fluctuations were always included in a linear form as only short gradients could be observed. Finally, interactions between the average water level and water level fluctuations were included.

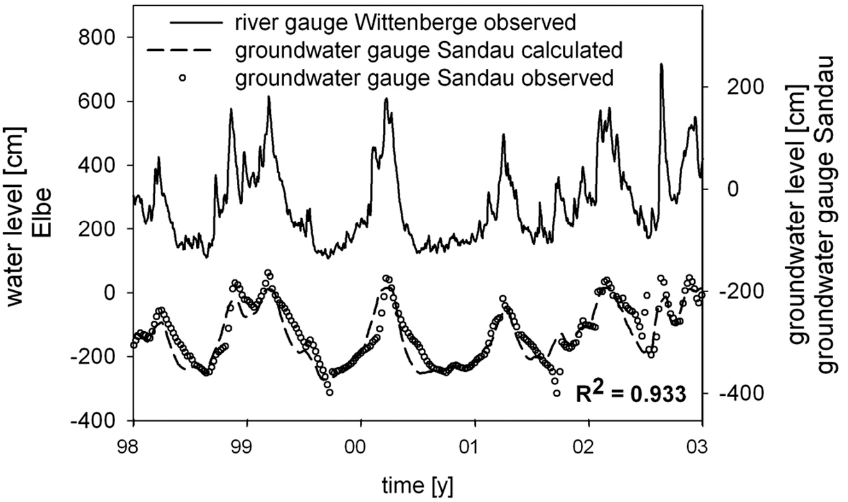

Figure 1: Hydrograph of daily water levels (1998–2003) at the gauges Wittenberge (Elbe River: observed) and Sandau (groundwater: observed vs. calculated). Calculated values for the groundwater gauge were derived from polynomial regression of observed groundwater gauge values as response variable and observed river gauge values as the predictor (R^2 displayed).

Model discrimination and model validation

To assess model performance we chose Nagelkerke's R^2_N (Nagelkerke 1991), which quantifies the proportion of variance explained by the model. For model discrimination, we applied a threshold-free criterion, the area under curve (AUC) of the receiver-operating characteristic (ROC), which is more reliable than arbitrary threshold-dependent measures, such as the correct classification rate, sensitivity or specificity (Fielding & Bell 1997). Model discrimination was evaluated according to Hosmer & Lemeshow (2000). Model validation, (i.e. testing model performance to evaluate the quality of a model) was performed internally by a bootstrapping procedure with 1000 iterations (Guisan & Zimmermann 2000) to correct for overoptimistic estimates of performance criteria, which can occur as a result of evaluation of model performance based on training data (dataset to set up models).

Further analyses

Differences in vegetation group occurrence (old trees, old shrubs, young trees, and young shrubs) were tested applying One-way anova with the average water level of the presence data as the response variable and vegetation group as the explanatory factor. Pair-wise comparison of vegetation groups was conducted by calculating Tukey's honestly significant differences (Crawley 2002). Normality of error structure and homoscedasticity was checked using diagnostic plots.

To compare actual species distribution with availability of potential habitat, a cut-off value (p_{krit}) for the probability of occurrence was applied to convert the values into a presence–absence dataset. While different possibilities for choosing cut-off values exist, we chose the sensitivity-specificity equality approach, i.e. the value for cut-off where the percentage of correct predictions for presences equals the percentage of correct predictions for absences ($=p_{\mathrm{fair}}$) (Liu et al. 2005).

All analyses were conducted in R (R Development Core Team, 2008). The HMISC and DESIGN packages were used for model estimation and validation (Harrell 2001).

Results

Model performance

All vegetation groups displayed comparatively low prevalences (= frequency of occurrence) with young life stages occurring rarely (old trees, 23.3%; old shrubs, 20.5%; young trees, 4.9%; young shrubs, 14.3%). All AUC-values of the models exceeded the critical value of 0.7 and were acceptable for old trees and outstanding (>0.9) for young shrubs. Overall, R^2_N

was higher for the shrubby vegetation type than for the tree type and more variation within the data could be explained for the young life stages than for the old stages (Table 1). Internal model validation by bootstrapping attained basically the same results as the training data set, so that the results can be considered well suited for predictive purposes (Table 1, see 'original' versus 'validated').

Effects of predictors

Vegetation types as well as age classes were influenced by the hydrological variables while their importance differed between types and age classes (for final models see Table 1). Both the vegetation types and the age classes were affected unimodally by the average water level, with each group exhibiting a different optimum (Fig. 2). In general, shrub communities were found on significantly lower elevations than trees, and young life stages occupied significantly lower sites than older life stages (one-way ANOVA: $F_{3,533}=106.96$, $P<0.001$, Table 2, Fig. 2). Furthermore, a significant interaction for shrubby vegetation was detected between the average water level and water level fluctuations. Where water level fluctuations were high (i.e. strong fluctuations of the water level occurred), old shrubs occupied areas with higher elevations (with a lower average water level, Fig. 3) compared to areas with lower fluctuations. Young shrubs were able to tolerate both lower and higher average water levels (Fig. 3) at sites of high water level fluctuations. In habitats with more stable water tables, fairly narrow average water level niches could be observed, so that the occurrences covered only a small part of the average water level gradient. For the trees, such patterns were not detectable (Fig. 3). As expected, land use had significant effects on both vegetation types and age classes, with decreasing probabilities of occurrence where there was mowing/grazing (Table 1). The effect of land usage was strongest for the young vegetation types and weakest for the old trees.

Comparison of actual and predicted habitat

Quantification of existing riparian softwood woodlands identified 64 stands ranging in size from 0.17 to 14.1 ha. The median size was 1.4 ha and all stands totalled approximately 178 ha, which was 2.5% of the study area (7272 ha).

Model extrapolation revealed large potential areas of suitable sites for old and young stages of both vegetation types (Fig. 4a, b). Generally, the area of suitable habitat was larger for the old life stages compared with the young life stages and the tree habitat covered a larger area than the shrub habitat (Table 3). Suitable habitat for mixed stands of both vegetation types covered large parts of the shrubby species habitat, while nearly 50% of the tree habitat was unsuitable for shrubby vegetation (Table 3).

Table 1: Regression coefficients, standard errors (SE) and p-values as well as performance criteria of the logistic regression models of the vegetation types and age classes.

	Trees					
	Old			Young		
	Coefficient	SE	*P*	Coefficient	SE	*P*
Intercept	-0.347	0.160	*	-0.775	0.236	**
AWL	-0.899	0.240	***	0.021	0.289	ns
AWL (quadratic term)	-0.886	0.132	***	-1.931	0.374	***
Mowing/ Grazing	-0.477	0.176	*	-1.662	0.442	***
Performance criteria	original	validated		original	validated	
R^2_N	0.194	0.187		0.345	0.331	
AUC	0.736	0.733		0.898	0.892	
	Shrubs					
	Old			Young		
	Coefficient	SE	*P*	Coefficient	SE	*P*
Intercept	1.451	1.051.	ns	-0.555	2.272	ns
AWL	5.020	2.076	*	12.681	4.315	**
AWL (quadratic term)	-11.371	2.532	***	-15.685	3.844	***
WLF	-1.036	1.038	ns	0.987	2.142	ns
Mowing/ Grazing	-0.988	0.192	***	-1.778	0.361	***
AWL^2*WLF	9.505	2.343	***	13.489	3.54	***
Performance criteria	original	validated		original	validated	
R^2_N	0.425	0.412		0.538	0.523	
AUC	0.873	0.870		0.922	0.918	

R^2_N: Nagelkerke's R^2; AUC: Area under Curve.

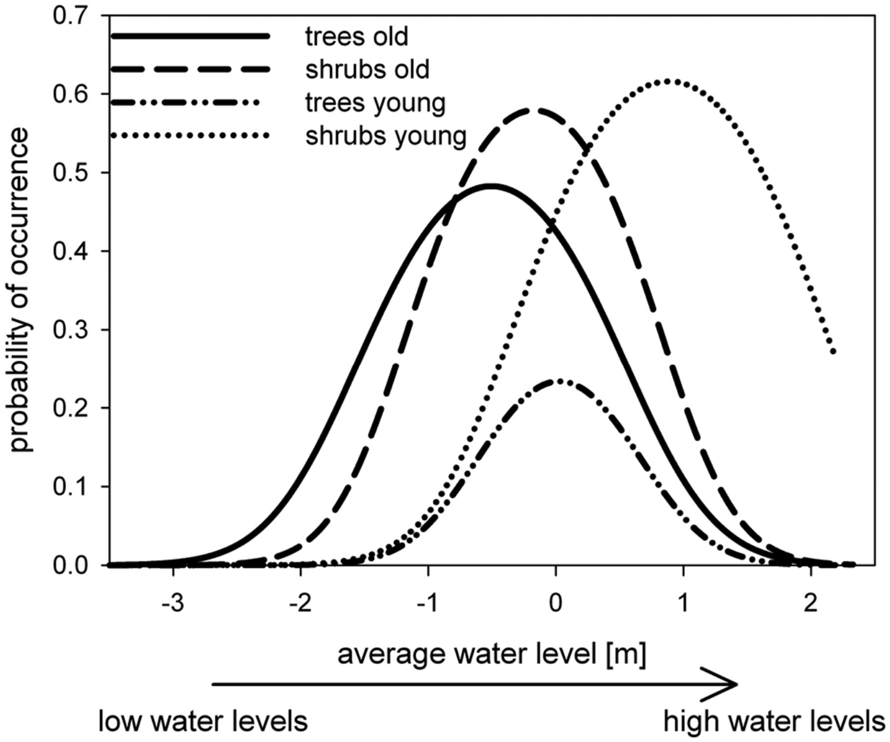

Figure 2: Probability of occurrence of vegetation types and age classes in relation to the average water level.

Table 2: Mean of the average water level (± standard error) for the presences of the vegetation types and age classes. Different letters indicate significant differences between means.

Species group	AWL mean ±SE
Trees old	-0.89 ± 0.003 [a]
Shrubs old	-0.59 ± 0.003 [b]
Trees young	-0.12 ± 0.013 [c]
Shrubs young	0.41 ± 0.070 [d]

Discussion

The distribution of vegetation in riparian woodlands is determined by hydrology and its interactions with other environmental variables (Van Splunder *et al.* 1995; Shafroth *et al.*

2000; Amlin & Rood 2002) in relation to the life-history stages of species (Braatne *et al.* 2007; Merritt *et al.* 2010; Stromberg *et al.* 2010). The distribution patterns and underlying mechanisms derived from such studies provide valuable background information for restoration.

Vertical zonation of floodplain vegetation

In general, the position of the vegetation types in relation to the average water level differed with trees occurring on higher, ‘drier’ sites. Such vertical zonation of floodplain vegetation along a gradient of flood duration and water levels has been recorded several times and is mainly explained by flooding tolerances and/or susceptibility of vegetation to desiccation after floodwater recession (Van Splunder *et al.* 1995; Amlin & Rood 2002); however, the models also revealed large overlaps in areas hydrologically suitable for tree and shrub habitat. In the study area, the zonation of extant softwood vegetation was very obvious along river banks and along non-permanent water bodies where high flow velocities occur during floods while in the flatter areas of the floodplain there was overlap between the two vegetation types. Consequently, it can be assumed that flood duration and high water levels as well as hydraulic forces restricted the niches for tree vegetation at low-lying sites. Bendix & Hupp (2000) also describe flood-prone sites, such as channel- or oxbow-shelves, as mostly being occupied by shrubby vegetation with resilient stems and high resprouting capability from flood-damaged stumps. Results of other studies support the hypothesis that there is greater growth vigour of floodplain shrubs compared with floodplain tree species under stressful abiotic conditions (Amlin & Rood 2001; Francis & Gurnell 2006). Sites at the river are hydraulically dominated whereas the adjacent terraces can be described as hydrologically dominated. The distribution of species is driven by hydro-geomorphological processes at the severe end of a stress–equilibrium gradient while at the other end of the stress gradient competition controls vegetation patterns (Gurnell 1997). Such processes might also explain the differences in the distribution of woody floodplain species along the elevational gradient.

Zonation patterns should be considered especially for areas facing strong hydraulic forces in times of floods. Shrubby softwood plantings should be placed along active channel shelves, flooding channels, and oxbows and trees should be positioned landwards to prevent damage from flooding or ice drift. Areas suitable for both vegetation types (i.e. the intersected parts of suitable habitats for trees and shrubs) should be selected for mixed plantings.

Hydrological niches of different life stages

Valuable restoration information can be derived from studies comparing the life-history requirements of young versus adult life stages of species (Braatne *et al.* 2007; Stromberg *et al.* 2010; Merritt *et al.* 2010). In this study, the habitats of the young versus adult life-history stages both were related to somewhat different hydrologies, with old vegetation occupying higher elevation habitats than younger vegetation. This included both the dendriform and the shrubby community types (*S. alba/x rubens* complex and Salicetum triandro-viminalis, respectively). Established woody vegetation is known to change riparian habitats by slowing river flow in times of floods. The hydraulic effect caused by woody vegetation leads to increased sedimentation and aggradation at vegetated sites over time (Steiger *et al.* 2005; Gurnell & Petts 2006; Nakamura *et al.* 2007). In addition, present-day reduction of hydro-geomorphological processes results in a lack of establishment sites for the young life stages and young individuals are mostly restricted to sites of high disturbance rates, such as river banks, oxbows or floodplain gullies. Consequently, a greater amount of suitable habitat of old life stages compared with the young life stages is identifiable.

Therefore, not only the spatial zonation of floodplain forests but also temporal succession processes should be considered. Environmental conditions of old and young stands can differ, as was demonstrated by Nakamura *et al.* (2007) for northern temperate floodplain forests in Japan. The establishment of *Salix* species at sites of old stands is impossible because water tables are too low to be reached by the small root system of younger plants originating either from seeds or cuttings/saplings (Van Splunder *et al.* 1995; Johnson 2000). Thus, planting sites should reflect site conditions of young life stages to guarantee sufficient water supply and to reduce dieback caused by desiccation of the cuttings/saplings (Francis *et al.* 2005). Sites of old life stages, at least in the floodplain where low flow velocities occur and former aggradation can be assumed, are presumably largely unsuitable for the development of cuttings/saplings.

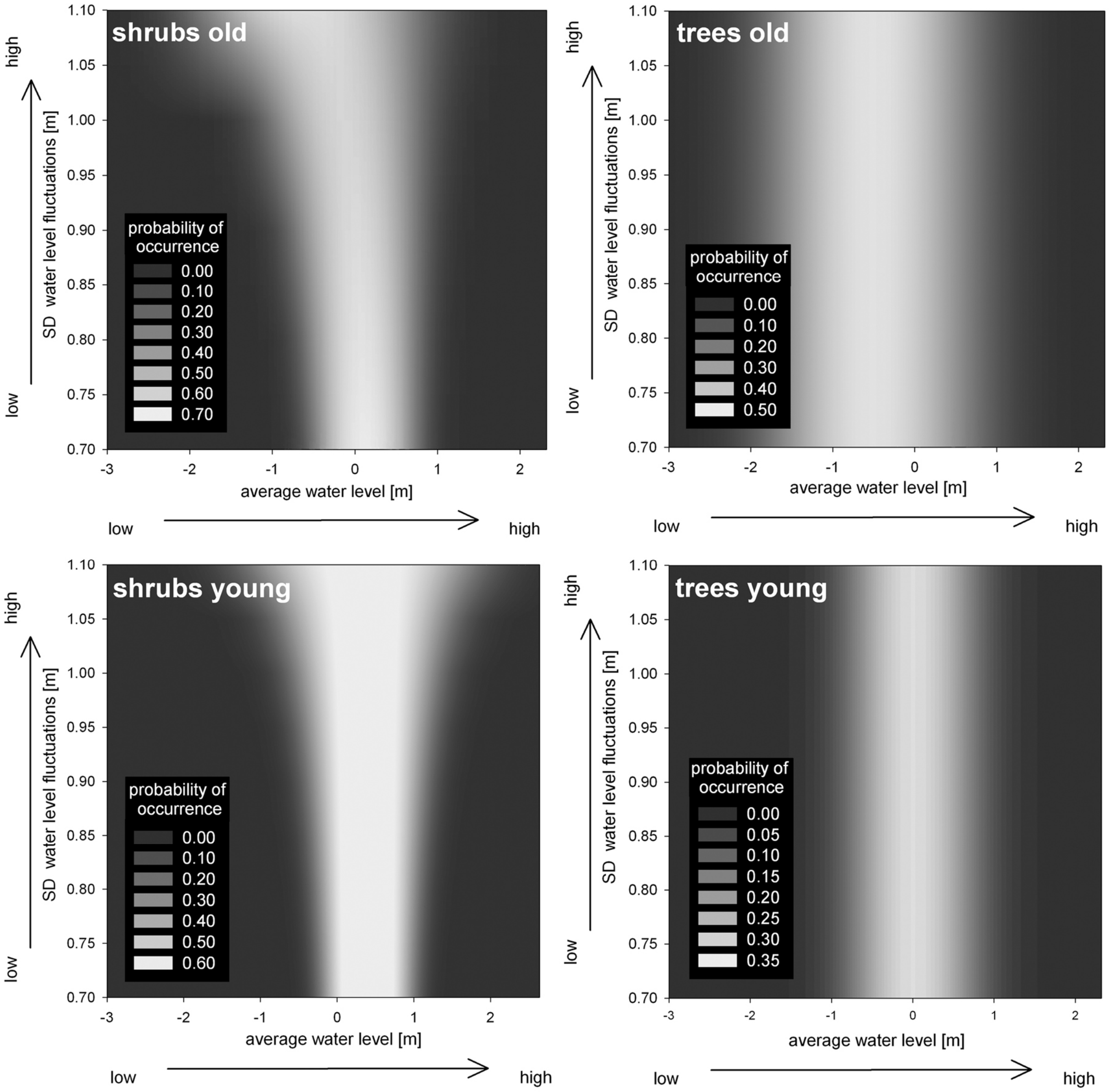

Figure 3: Probability of occurrence of vegetation types and age classes in relation to the interaction of the average water level (x-axis) and water level fluctuations (y-axis).

Table 3: Calculated area/percentage of whole floodplain of suitable habitat for the different vegetation types and age classes based on $p_{krit}= p_{fair}$; A) For each vegetation type and age class; B) For merged vegetation types within age classes (suitable habitat for group x only + suitable habitat for group y only + intersection area of suitable habitat for group x + group y), C) For intersected vegetation types within age classes (suitable habitat for both group x + group y), and D) Percentage of suitable habitat of each vegetation type and age class based on mixed vegetation stands in relation to entire suitable habitat available for each single vegetation type and age class.

Vegetation type	A Calculated area [ha]/ Percentage of whole floodplain	B Calculated area [ha] of merged groups/ percentage of whole floodplain	C Calculated area [ha] of intersected groups/ percentage of whole floodplain	D Ratio of area C to A [%]
Trees old	2858 / 39.3 %	3017 / 41.5 %	1565 / 21.5 %	54.5 %
Shrubs old	1724 / 23.7 %			90.8 %
Trees young	2033 / 28.0 %	2267 / 31.2 %	1141 / 15.7 %	56.1 %
Shrubs young	1376 / 18.9 %			82.9 %

The role of interactions in identifying suitable habitat

Another major finding relevant for identifying suitable habitats for woodland reforestation was the interaction of the average water level with water level fluctuations observable for old and young shrubs. At locations where water levels strongly fluctuated, for example, along the active channel shelf or on floodplain banks, the species were found at a wider range of different elevations compared with sites where fluctuations were smaller. Obviously, high elevation sites of stagnant water conditions exhibit drought stress and the species' survival rates increase at lower lying sites with shallower average water levels. At sites close to the river, this problem is less pronounced because stronger water level fluctuations lead to recurring moist soil substrate. Trees did not show this dependency, demonstrating that this softwood woodland vegetation type is less prone to water deficiencies (Amlin & Rood 2002; Francis *et al.* 2005). Similar results have been documented by Shafroth et al. (2000) where saplings of North-American *Populus fremontii* and *Salix gooddingii*, both typical riparian tree species, were found to be strongly affected not only by the average water table depth but also by inter-annual changes of the water table depth. At sites with greater depth to groundwater and inter-annual fluctuations, sapling survival was greater compared with sites with fairly stable, shallow water tables. Differences in response patterns to interaction between water level and fluctuation were also reported by Leyer (2005) for grassland species. Here, species occurrences in the areas of the old floodplain exhibiting reduced fluctuations were bound to the middle of an elevational gradient. This pattern of species occurrence was primarily because of increased drought at higher elevations and tendencies towards permanent inundation at low-lying sites, in contrast to wider elevational niches in the active floodplain. Similarly, in this study, this pattern was also clearly demonstrated for both life stages of the softwood shrubs. Thus, appropriate sites for woodland reforestation for softwood shrubs need to be chosen carefully, where water level fluctuations are small, for example, in areas far away from the river and flooding channels. The positioning of plantings may be of particular importance for the area behind the dykes (the inactive floodplain) where water level fluctuations are lower (Leyer 2004, 2005). In Germany, the Netherlands and other European countries, reforestation in the active inundation area and particularly close to the river, is often prevented by stakeholders, such as water authorities who have concerns about threats from increased flooding risk. Therefore, sites behind the dykes are often given priority for softwood woodland plantings. We recommend paying special attention to the fact that the niche along the elevational gradient where softwood shrubs can grow is much smaller here than in the active floodplain. While high elevation sites might be too dry to allow saplings or cuttings to become established, low-lying areas could have water tables too stagnant for softwood shrub establishment.

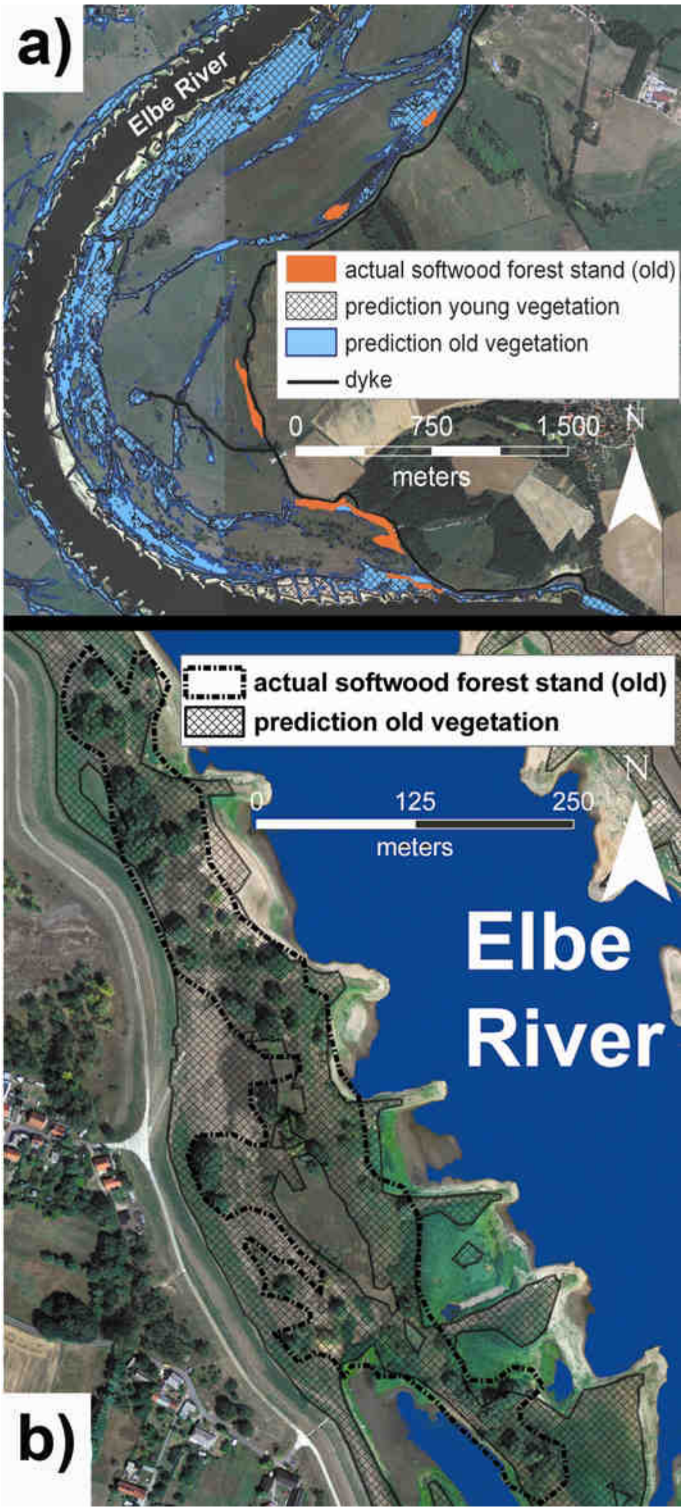

Figure 4: a) Predictions of young and old vegetation (intersection of vegetation types) and actual stands of old softwood forest vegetation (trees and/or shrubs) for a portion of the study area (young stands not present in this river section). b) Detailed view of actual old stand with scattered trees and shrubs and predictions of old vegetation (intersection of vegetation types).

Conclusion and Perspectives

Rivers are temporally and spatially highly dynamic systems and species distribution in general is controlled by a great variety of factors. We demonstrated that simple hydrological variables are sufficient to describe occurrence patterns of riparian softwood species when life stages and interactions between variables are considered. Thereby, suitable reforestation sites for riparian *Salix* plantings can be identified. While the specific relationship between the vegetation groups investigated and hydrological conditions should not be adapted to other river systems without model validation, this method might be helpful to increase the success of reforestation for regeneration of riparian softwood communities.

Restoration of the mechanisms (e.g. the river flow dynamics and the variety of geomorphological processes) leading to vital, self sustainable floodplain ecosystems with natural recruitment of floodplain forests should be the goal of restoration efforts (Hughes *et al.* 2001). However, on a broad scale, and especially for river systems such as the Rhine, Elbe or Danube River, where economical interests (navigation, agriculture, flood protection, and power production) prevail, such measures are often not feasible (Buijse *et al.* 2002). Thus, planting tree saplings may be the only means to conserve and restore riparian softwood woodlands along large rivers in Central Europe, as is requested by the aims of the EU Water Framework Directive or the EU Habitats Directive, among others. Moreover, planting acts as a short-term measure where success can be achieved much faster than the restoration of natural river flow dynamics (Stanturf *et al.* 2001). Prompt action to preserve the potential for either generative or vegetative dispersal is necessary because the individuals in remnant stands along most rivers in Europe are old (Tockner & Stanford 2002). Furthermore, many stands are exposed to various other threatening processes, which, if not addressed with conservation and restoration measures in the near future, may lead to the permanent loss of these systems. Fragmentation of remnant stands exposes them to various problems, such as small stand sizes with high extinction risk, disruption of pollination processes for dioecious species (all *Salix* species investigated) or loss of species identity as a result of boosted hybridization processes, as has been observed for *Populus nigra* (Ziegenhagen *et al.* 2008). Further reduction in population size and increased fragmentation might lead to failure of dispersal processes of generative and vegetative propagules (Van Eck *et al.* 2005). Restoration of hydro-geomorphological processes is necessary to maintain self-preserving floodplain systems in the long term. For short-term projects, planting may contribute to the sustainability of riparian woodlands in Central Europe.

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Chapter 3

Vegetative reproduction capacities of floodplain willows – cutting response to competition and biomass loss

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Abstract

While several studies on regeneration in Salicaceae have focused on seedling recruitment, little is known about factors controlling their vegetative reproduction. In two greenhouse experiments, we studied the response of floodplain willows (*Salix fragilis*, *S. viminalis*, *S. triandra*) to competition with *Poa trivialis*, and to shoot and root removal when planted as vegetative cuttings. In the first experiment, growth performance variables were analysed in relation to full competition, shoot competition, root competition and control, taking into account two different water levels. After 9 weeks, shoots were removed and the resprouting capacity of the bare cuttings was recorded. In the second experiment, the cutting performance of the three floodplain and an additional two fen willow species (*S. cinerea*, *S. aurita*) was compared when grown in three different soil compositions and with two different water levels. After 9 weeks, shoot and root biomass was removed and the bare cuttings were replanted to test their ability to resprout. Cutting performance and secondary resprouting were negatively affected by full and shoot competition while root competition had no or weak effects. The floodplain species performed better than the fen species in all soil types and water levels. Secondary resprouting capacity was also higher in the floodplain species, which showed an additional strong positive response to the previous waterlogging treatment. The results contribute to understanding of the vegetative regeneration ecology of floodplain willows, and suggest that the use of cuttings in restoration plantings could be an effective strategy for recovering floodplain forests.

Introduction

In past centuries, willows and poplars formed large floodplain forests along all major rivers in Central Europe (Hager & Schume 2000) and played important roles as the first woody species to colonise and stabilise sites disturbed by flooding and sedimentation/erosion processes. Today, these so-called softwood forests are in steep decline as most large rivers are severely impacted by river regulation and floodplain fragmentation due to dams and dykes which are restricting flow-induced disturbances and subsequent regeneration (Nilsson & Bergren 2000; Tockner & Stanford 2002).

Willows have small, short-lived seeds and sexual reproduction is controlled by various factors such as the presence of competition-free, bare-ground sites, sufficient moisture in combination with suitable soil substrates, no burial by sedimentation and no extended submersion by flooding during the growing season (Karrenberg *et al.* 2002). Thus, a lack of bare-ground sites due to the lack of natural disturbances along regulated rivers leads to limited or even absent sexual reproduction (Scott *et al.* 1997). However, European woody floodplain species such as *Salix fragilis*, *S. viminalis* and *S. triandra* are well known for their ability to regenerate vegetatively. Whenever fragments of branches fall into the water and are swept away by the current, they can usually resprout as soon as they are deposited onto a suitable patch of ground (Beismann *et al.* 1997, 2000; Barsoum 2002).

While several studies on regeneration in Salicaceae have focused on seedling recruitment (van Splunder *et al.* 1996; Guilloy-Froget *et al.* 2002; Karrenberg *et al.* 2002), little is known about factors controlling the establishment of vegetative recruits. Some studies have examined the role of abiotic variables such as inundation/drought on the establishment of vegetative propagules under controlled conditions (Barsoum & Hughes 1998; Amlin & Rood 2001, 2002) and field investigations have revealed that asexual recruits have a wider spatial distribution within the floodplain because they tolerate broader environmental conditions than seedlings (Barsoum 2002; Moggridge & Gurnell 2009). However, biotic interactions such as competition have been widely ignored.

Pioneer habitats in natural floodplains are generally poor in vegetation, *i.e.* competition is not a major factor shaping pioneer community composition. However, man-made alterations in the flow regime lead to increased stability in formerly dynamic floodplain habitats. Accordingly, succession proceeds which results in pioneer species experiencing competition (Rood & Mahoney 1990; Nakamura & Inahara 2007). To better understand the mechanisms behind competition, the effects of above and/or belowground competition have been studied separately (Gurevitch *et al.* 2006), but until now vegetative propagules have not been in the focus of these studies.

During the establishment phase, willow seedlings exhibit slow growth rates and only limited resprouting ability, which renders the sexual regeneration strategy susceptible to sedimentation and mechanical impacts caused by floods (Barsoum 2002). In contrast, vegetative propagules have carbohydrate reserves and pre-formed root and shoot primordia (Schier & Campbell 1976), which should be an advantage for resprouting when river-induced disturbances or beaver herbivory lead to the loss of shoots and/or roots. However, beyond the general statement that species of this genus can resprout easily, there is no information as to how vegetative recruits actually react to such disturbance events.

As human-induced habitat alterations have increasingly impacted the sexual regeneration ability of floodplain willows, vegetative propagation has inherently become more important for the maintenance of populations. Therefore, the aim of this study was to contribute to a better understanding of the vegetative reproduction capacities of floodplain willows by analysing firstly the effects of above- and belowground competition using *Poa trivialis* as the competing species, secondly the effects of shoot and complete (shoot and root) biomass removal on plant performance, respectively; and thirdly, evaluate whether floodplain willows are more adapted for vegetative propagation than willows found in fen habitats. In two controlled greenhouse experiments the following questions were addressed:

1 Does aboveground and belowground competition affect establishment rates and growth performance of floodplain willow cuttings?

2 Are there different responses to aboveground and belowground competition within and among different species?

3 Are willow cuttings able to resprout a second time after shoot removal under competition conditions?

4 Do floodplain willows have better resprouting capacities than fen willows after shoot and root removal?

Methods

Study species

The tree-forming Crack Willow (*Salix fragilis* L.) and two shrub-like species, the Oiser (*S. viminalis* L.) and the Almond Willow (*S. triandra* L.), were chosen as representatives of riparian softwood forests of Central Europe. Additionally, two fen habitat species, Grey Willow (*S. cinerea*) and Eared Willow (*S. aurita*), were chosen to compare resprouting capacities among willows of different habitats. All five species are supposed to have a high capacity for vegetative regeneration (Schiechtl 1992). Since the resprouting ability changes over the course of the year, reaching its maximum at the end of winter dormancy (Schiechtl 1992), cuttings were harvested at the end of January 2008 at the Lahn River, near Marburg, and in a fen north of Marburg, Hesse, Germany. Following literature recommendations (*e.g.* Chmelař & Meusel 1986), the diameter and length of the collected cuttings ranged between 4 and 11 mm and between 13 and 23 cm, respectively. Twigs were harvested from five individual trees per species. The species identity of the selected *S. fragilis* individuals was genetically determined prior to harvesting using consensus primers based on exon sequences of the cyp73 gene family according to Trung *et al.* (2008) (Neuschulz, E.L., personal communication), as morphological identification of this species and its hybrid *S.* × *rubens* is difficult. The experimental set up in the greenhouse was started immediately after harvest. Temperature and light conditions were kept constant at 15–20°C and 12 h a day throughout the whole experiment.

Poa trivialis L. s.l., purchased from a commercial supplier (*Poa trivialis* Z., Rieger-Hofmann GmbH, Blaufelden-Raboldshausen, Germany), served as the competing species. It is a flood-tolerant, tussock-forming grass that produces a dense root system and occurs frequently in riparian areas and other wetlands.

Design of the 1st experiment: competition and shoot removal

Cuttings of the three target species (*S. fragilis*, *S. viminalis*, *S. triandra*) were subjected to four competition and two water treatments in a full factorial design. Competition treatments comprised four levels: (i) control: target species only; (ii) root competition: interaction between target and neighbour species (*P. trivialis*) – with no shoots of the neighbour species; (iii) shoot competition: interaction between target and neighbour species – with no roots of the neighbour species (neighbour species replaced by plastic fronds); and (iv) full competition: interaction between target and neighbour species with both shoots and roots. The factor 'water level' was included to account for elevational differences in willow habitats, with either waterlogged soil (water level at the soil surface) or moist soil (water level approx. 3 cm below the soil surface with a total soil depth of 4 cm). Each factor combination was replicated five times (N = 40 per species).

To start the experiment with a defined grass density, 20 ml of *P. trivialis* seeds were sown into each PVC box 3 months in advance. For the root competition treatment, the pre-grown grass was cut directly above the surface at the start of the experiment and subsequently every 2 weeks. The shoot competition treatment was realised with 55 matt-green-foiled fronds per box, creating a similar amount of shade as the grass in the full competition treatment. There, the grass was maintained at the 18-cm height of the fronds. Cuttings were placed horizontally onto the soil surface of the PVC boxes, with five twigs of the same species per box, *i.e.* one twig of each of the field-sampled individuals per species. The boxes were filled with a soil mixture of 15% gravel, 35% humus and 50% sand and were placed in trays to apply the two different water levels. To avoid local effects, all the boxes were located randomly in the greenhouse and shuffled from time to time. The soils were fertilised once a week with a universal N-P-K fertiliser and the grass was treated regularly against powdery mildew (BioBlatt, Neudorff GmbH KG, Emmerthal, Germany). To prevent feeding damage caused by caterpillars and leaf miners, a biological broadband insecticide (Spruzit®, Neudorff GmbH KG, Emmerthal, Germany) was applied once only.

Four response variables were measured for each cutting: (i) the cumulative number of sprouts emerging; (ii) the length of the longest sprout emerging; (iii) the total sprout length as the sum of all sprouts; and (iv) the total aboveground biomass produced by this cutting. The multi-measured variables (i–iii) were gathered three times: at 2 weeks, at 4.5 weeks and at 8.5 weeks. After 9 weeks, shoot biomass was cut without moving the cuttings and touching the roots, oven-dried in paper bags for 1 week at 40 °C and weighed. It was not possible to measure the root biomass because the root system of *P. trivialis* was very dense and intertwined with the willow roots.

To assess the capacity of the cuttings to resprout a second time after the shoot biomass removal, they were left in the boxes with the previous competition treatments. Four weeks later, the number of cuttings that had resprouted again was counted.

Design of the 2nd experiment: soil types and removal of shoots and roots

A second experiment was set up to obtain a better idea of the resprouting capacities of floodplain willows in comparison to fen willows, especially after shoot and root removal. Cuttings of the three floodplain and the two fen willows were planted in 3-L PVC pots in three different soil types and were subject to two water level treatments with four replicates per factor combination (N = 24 per species). To cover the whole range of soil types occurring in floodplains, the following soil compositions were chosen: a gravel–sand mixture (45% gravel, 45% sand, 10% humus), loam (30% sand, 30% silt, 30% clay, 10% humus) and a peat–sand mixture (50% sand, 50% humus/peat). Pots were placed in slightly larger buckets to apply two different water levels: waterlogged (water level at the soil surface) and moist (water level approx. 3-cm high). Since a preliminary study revealed that horizontally placed cuttings resprout as well as vertically placed cuttings, cuttings of the second experiment were planted vertically for reasons of space. Per pot, four cuttings of the same species but of different individuals were inserted into the soil to three-quarters of their length. To avoid local effects, all buckets were located randomly in the greenhouse and shuffled from time to time. To prevent damage by caterpillars or leaf miners, the twigs were treated as described in the first experiment.

After 9 weeks, the shoot and root biomass of each cutting was harvested, separately oven-dried in paper bags for 1 week at 40°C and weighed. To test secondary resprouting potential, the bare cuttings were horizontally laid on the soil surface in 1 × 1 m PVC trays filled to 4 cm with a soil mixture of 15% gravel, 35% humus and 50% sand. The water level was maintained at a height of about 2 cm. The cuttings were randomly distributed among trays regardless of previous treatment. Due to individual labelling of the cuttings, previous treatments could be related to secondary resprouting performance. Four weeks later, the number of cuttings that had resprouted again was counted and the shoot biomass was cut, dried and weighed following the procedure described above.

Data analysis

In the first experiment, the effects of species, competition and water level on aboveground biomass were tested with a three-way factorial ANOVA, with box as the unit of replication. Response variables were square root- (or rarely log-) transformed when they failed to meet the assumptions of homoscedasticity and/or normality of errors, which was checked using diagnostic plots (Crawley 2002). Multiple comparisons among factor levels were calculated with a Tukeys'*post hoc* test. To test the effects of species, competition and water level on the multi-measured variables (i–iii), linear mixed models (LMM; Crawley 2007) were used with repeated measures as the random factor. Subsequently, a multiple comparison test (Tukey-style) for parametric models was employed to detect differences among the competition treatments for each species averaged over water level (Hothorn *et al.* 2008). Secondary resprouting capacity (number of cuttings that resprouted after shoot removal/number of cuttings that resprouted before) was compared pair-wise among species and competition levels using binomial proportion tests (Crawley 2002).

In the second experiment, the effects of species, soil type and water level on shoot and root biomass of primary resprouting, as well as on shoot biomass of secondary resprouting were tested with three-way factorial ANOVAS followed by Tukeys'*post hoc* tests, with pots as the unit of replication. Secondary resprouting capacity was compared pair-wise among species with binomial proportion tests (see above).

Data analyses were carried out using the software package R (Version 2.12.1, R Development Core Team 2010, Vienna, Austria). For LMM and related multiple comparisons, the *lmer* function in the software package *lme4* (Bates & Maechler 2010) and the *glht* function in the software package *multcomp* (Hothorn *et al.* 2008) were used, respectively.

Results

Cutting responses to competition and shoot removal (1st experiment)

All three target species showed very high establishment rates (proportion of established cuttings): *S. viminalis*: 99.5%, *S. fragilis*: 97.0%, *S. triandra*: 94.5%. The number of sprouts emerging from one cutting clearly decreased over time (Fig. 1a–c) varying among species and competition treatments (Table 1). The cuttings of *S. fragilis* and *S. viminalis* had fewer sprouts when grown with full or shoot competition, and in the case of *S. triandra*, when grown with full competition in comparison to the control (Fig. 1a–c).

After 9 weeks, some single sprouts had reached a length of 1 m. The length of the longest sprout per cutting did not differ among species or water levels, but competition had a large effect on length (Table 1). In all three species, the length of the longest sprout was significantly lower when cuttings were grown with full competition. This negative effect was greatest in *S. triandra* and smallest in *S. fragilis* (Fig. 1d–f).

The total length of all sprouts per cutting (sum of length of all single sprouts) differed greatly among species and even more among the treatments (Table 1). The sprout lengths of all studied species were larger when grown with shoot or full competition than with root competition or in the control (Fig. 1g–i).

The aboveground biomass differed among species, competition treatments and water levels (Table 1). Shoot and full competition had a clear negative effect on the aboveground biomass of the cuttings, whereas there was no difference between root competition and the control (Fig. 2). Even though the ANOVA indicated the strong effect of water level, it was only substantial for *S. fragilis*, which produced more biomass under waterlogged conditions (Fig. 2).

Regarding the secondary resprouting capacity after removing the sprouts, *S. fragilis* had lower failure rates than the other two willow species (Table 2a). Additionally, failure rates were higher in full competition than in any other competition treatment (Table 2b).

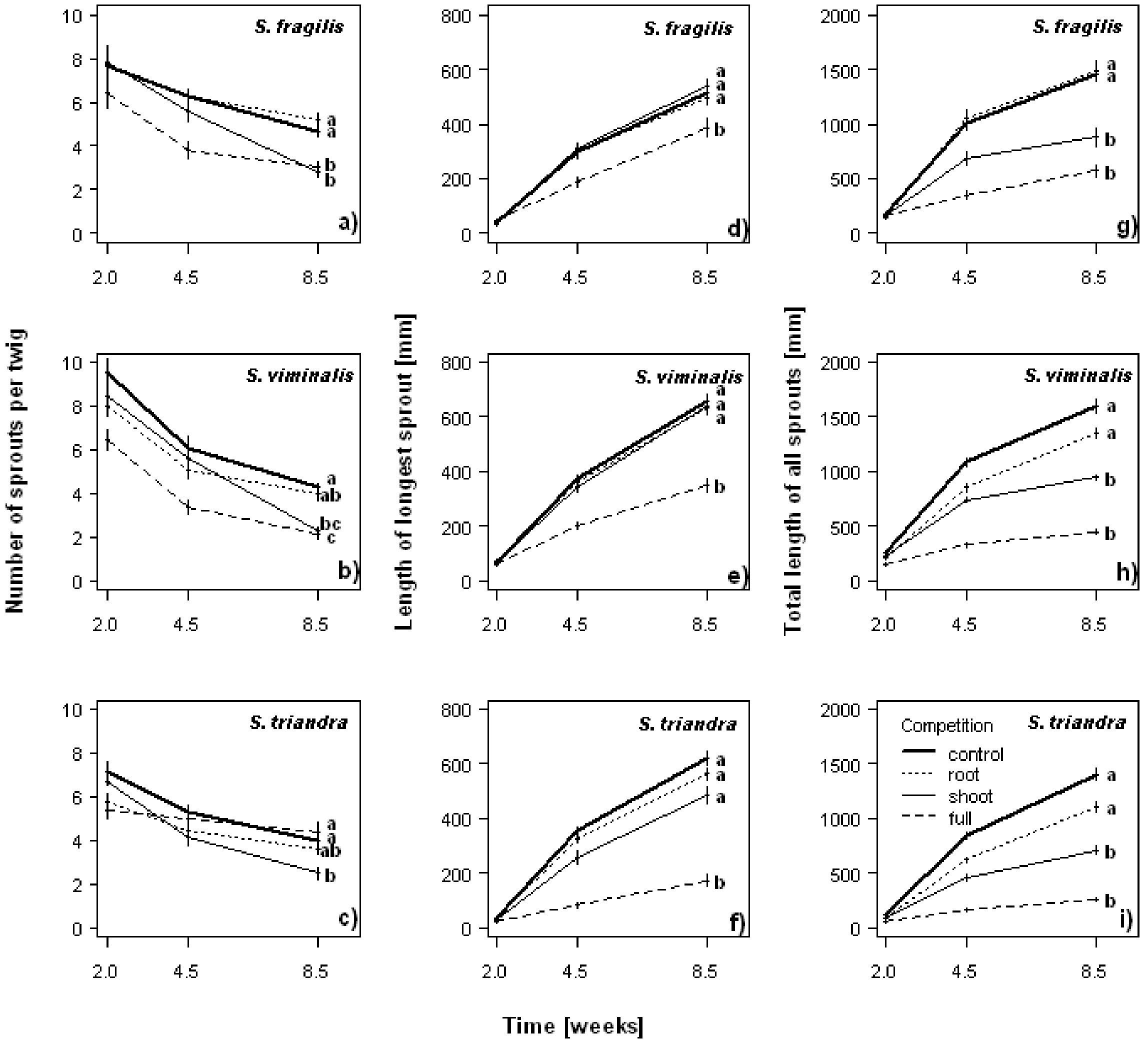

Figure 1: Competition effects on different performance criteria of the three investigated floodplain species (1^{st} experiment). (a–c): Effects on the number of sprouts per cutting (means ± SE); (d–f): effects on the longest sprout per cutting (means ± SE); (g–i): effects on the total length of all sprouts per cutting (means ± SE). Different letters indicate differences ($P < 0.05$) after multiple comparison procedures. Data on water level were pooled because they had no significant effect in LMM.

Table 1: Main effects (species, competition, water level) and their interactions on multi-measured variables in the 1st experiment: number of sprouts, length of longest sprout per cutting and total length of all sprouts per twig (LMMs), as well as on biomass (three-way ANOVA). Values are F-values. Levels of significance (P) are denoted, *P < 0.05, **P < 0.01 and ***P < 0.001.

	d.f.	N° of sprouts (LMM)	Longest sprout (LMM)	Total length (LMM)	Shoot biomass (ANOVA)
Species	2	7.34**	0.10	4.59*	20.00***
Competition	3	26.27***	64.16***	47.85***	155.99***
Water level	1	0.05	0.07	0.24	30.09***
Spec:comp	6	8.27***	5.35*	0.41	1.13
Spec:water	2	4.02*	1.67	0.82	13.16***
Comp:water	3	3.51*	1.98	0.19	1.98
Spec:comp:water	6	0.92	0.22	0.05	2.31*
Residuals	96				

Cutting responses to soil type and shoot and root removal (2nd experiment)

All five species (floodplain and fen willows) showed very high resprouting rates after initial planting: *S. viminalis* and *S. fragilis* 100%, *S. triandra* 96.9%, *S. aurita* 99%, and only *S. cinerea* had a significantly lower resprouting rate (92.7%; proportion test, P < 0.05).

Aboveground biomass (primary resprouting) differed among species and soil types; belowground biomass was affected by water level (Table 3). Floodplain species clearly performed better than Fen species, regardless of soil and water treatment. Among fen species, *S. aurita* performed significantly worse than *S. cinerea* (Fig. 3a–d). The shoot biomass of the floodplain species increased from sand, through loam to peat soils (Fig. 3a and c). The shoot biomass responses of *S. cinerea* and *S. aurita* to the soil types differed. All species produced more root biomass under moist than under waterlogged conditions (Fig. 3d).

As regards the secondary resprouting capacity after shoot and root removal, the three floodplain willows had clearly higher resprouting rates (95 – 98%) than the fen species (63–64%; Table 4). The secondary shoot biomass depended on the species (floodplain species produced more biomass than fen species, Fig. 3e and f) and, remarkably, on previously applied water treatment (Table 3), *i.e.* floodplain willow cuttings previously grown under waterlogged conditions produced more secondary shoot biomass than those grown under moist conditions. This was in contrast to the primary shoot and root production patterns, which reflected no or negative effects of waterlogging (Fig. 3b and d).

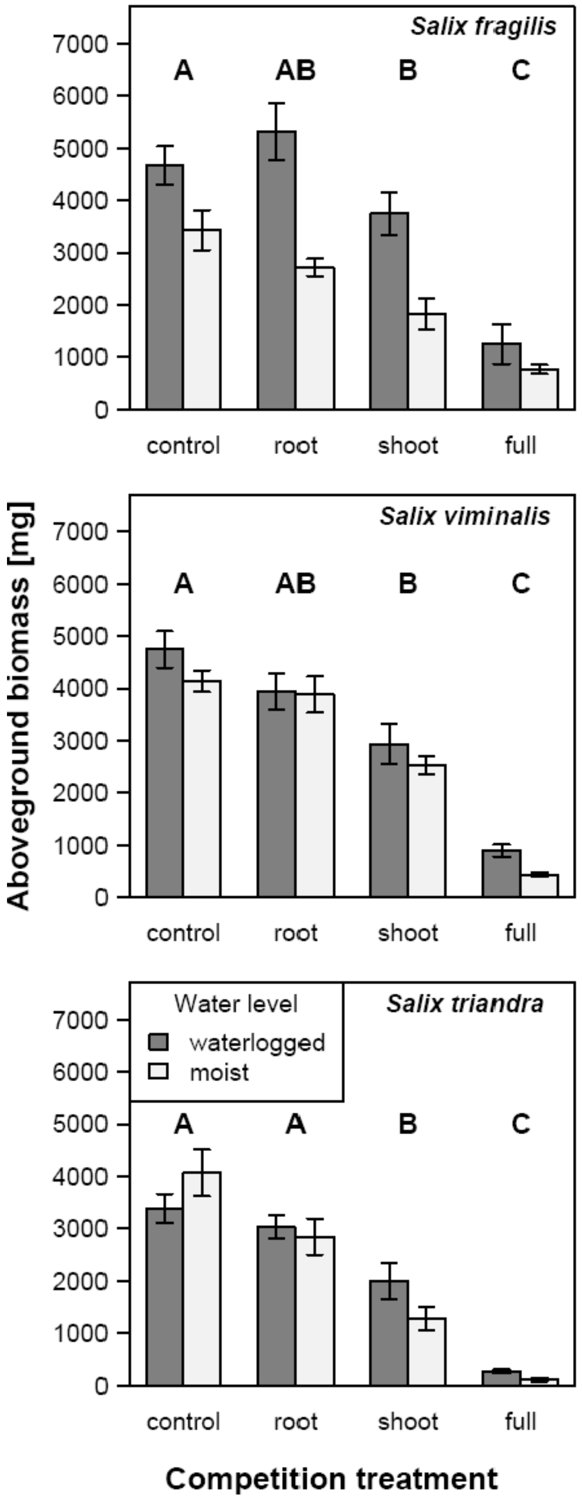

Figure 2: Effects of competition and water level on aboveground biomass (means±SE) of the three target species (1st experiment). Different letters indicate Tukeys' HSD among competition treatments (p<0.05).

Table 2: Secondary resprouting results of the 1st experiment (competition and shoot removal) for a) the three target species regardless of treatment, and b) the four competition treatments pooled over species and water treatment. Diagonal values: number of cuttings that resprouted a second time/number of cuttings that resprouted the first time. Other entries are Chi-square values of the pair-wise proportion tests, *P < 0.05 and ***P < 0.001 (df = 1). Bottom letters indicate the differences.

a) Comparison among species

	S. fragilis	*S. viminalis*	*S. triandra*
S. fragilis	176/194	4.02*	9.62***
S. viminalis		166/199	1.05
S. triandra			149/189
	a	b	b

b) Comparison among competition treatments

	control	root	shoot	full
control	143/148	1.4	0.74	93.04***
root		141/142	4.93*	102.51***
shoot			136/145	79.57***
full				66/147
	a/b	a	b	c

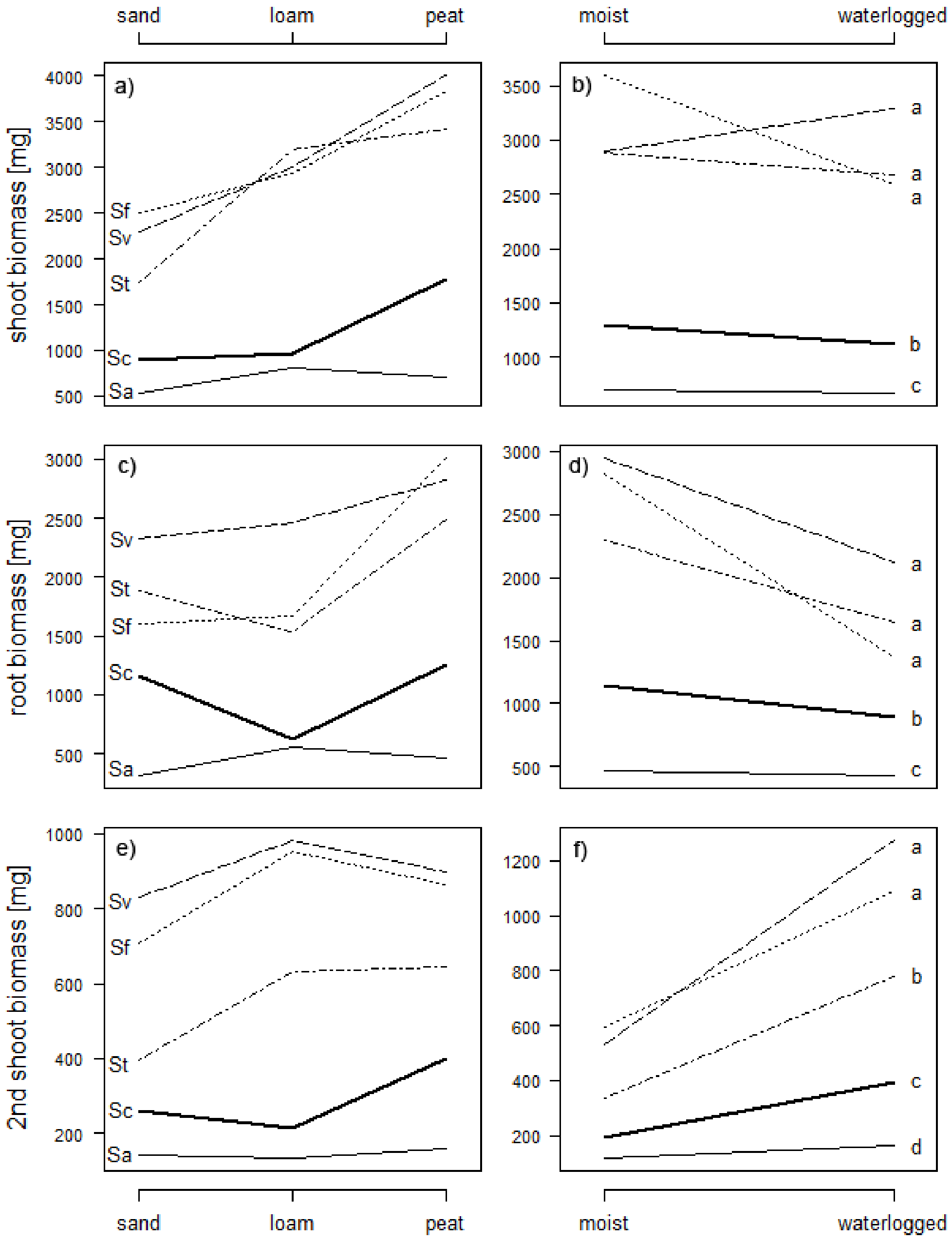

Figure 3: Interaction plots for the 2nd experiment with soil types and species (a,c,e) as well as water level and species (b,d,f), showing their effects on shoot biomass (a,b), root biomass (c,d) and secondary shoot biomass (e,f). Solid lines indicate fen species (Sc –*S. cinerea*; Sa –*S. aurita*), dashed lines indicate floodplain species (Sf –*Salix fragilis*; Sv –*S. viminalis*; St –*S. triandra*). One line type indicates the same species in all six sub-figures. Different letters on the right indicate Tukey's HSD among species (regardless of soil type or water level in which they were grown).

Table 3: Main effects of species, water level and soil type as well as their interactions on shoot biomass, root biomass (both primary resprouting) and secondary shoot biomass (produced after root and shoot removal) in the 2nd experiment. Values are F-values of three-way ANOVAs. Levels of significance (p) are denoted with *p<0.05, **p<0.01 and ***p<0.001. The transformation method used to improve the diagnostic plots is given in the column head.

	d.f.	Shoot biomass (log)	Root biomass (log)	2nd Shoot biomass (sqrt)
Species	4	142.61***	54.11***	71.87***
Water	1	0.29	9.81**	107.52***
Soil	2	30.36***	5.49**	4.15*
Species:water	4	1.63	0.81	4.58**
Species:soil	8	3.06**	2.62*	1.60
Water:soil	2	1.40	0.30	0.06
Species:water:soil	8	2.90**	1.38	0.69
Residuals	90			

Discussion

It is well documented that woody floodplain pioneers, such as willows and poplars, require competition-free, bare sediments and suitable hydrological conditions to establish from seeds (*e.g*. Lautenschlager 1994; Scott *et al.* 1997). The results of this study indicate negative effects of competition for vegetative reproduction as well. All three floodplain species were adversely affected by aboveground and full competition, whereas root competition had no or only weak effects. Secondary resprouting performance after shoot removal was lower with aboveground and full competition. This might be caused by direct effects (*e.g.* shading) or by indirect effects through weakening of the cuttings due to prior competition. It appears that aboveground competition acts more strongly than belowground competition on willow cuttings in the experiment, which is a characteristic of nutrient-rich habitats (Belcher *et al.* 1995) such as floodplains – or in this case – the fertilised soils of the experiment. In productive habitats, aboveground biomass production is intensified and the effect of shading, and therefore the strength of shoot competition, becomes more important

(Twolan-Strutt & Keddy 1996; Gurevitch *et al.* 2006). In contrast, the strength of root competition decreases since nutrient availability is not limited (Casper & Jackson 1997).

Table 4: Secondary resprouting results of the 2nd experiment (shoot and root removal). Diagonal values: number of cuttings that resprouted a second time / number of cuttings that resprouted the first time. Other entries are Chi² values of pairwise proportion tests with ***p<0.001and d.f. = 1. Letters at the bottom summarise the differences.

	S. fragilis	*S. viminalis*	*S. triandra*	*S. cinerea*	*S. aurita*
S. fragilis	92/96	0.17	0	27.35***	29.40***
S. viminalis		94/96	0.66	32.63***	34.74***
S. triandra			88/93	23.99***	25.93***
S. cinerea				58/90	0
S. aurita					60/95
Group	a	a	a	b	b

The question arises as to how important the observed competition effects are for preventing the establishment of willow cuttings. Growth rates of the longest sprouts were generally high, except for the full competition treatment, with some sprouts reaching 1 m within 9 weeks. Under natural conditions, this property offers the chance of cutting survival even under moderate competition and under flood conditions by escaping from shade, being buried and being under water. With respect to water availability, cuttings showed no or weak responses to applied water levels, indicating the tolerance to a rather broad range of moisture conditions. These findings indicate that vegetative propagules of floodplain willows are less susceptible to unfavourable growing conditions, such as the mechanical impacts of floods, burial and drought stress, compared to seedlings (Barsoum 2002). Cuttings can tolerate broader environmental ranges than seedlings and usually have higher survival rates (Moggridge & Gurnell 2009). It is even possible that willow forests establish along rivers only by vegetative reproduction, as found in a genetic study on willows of the *S. alba*–*S. fragilis* complex in Patagonian river systems (Budde *et al.* 2010).

This study shows further showed that even when shoot and roots are removed from cuttings only 9 weeks after establishment, they vigorously resprout a second time. Projecting this phenomenon into a dynamic floodplain implies that already established vegetative propagules can be uprooted and translocated again without losing their resprouting potential. This trait was especially striking in the floodplain willows when compared to the fen willows, clearly reflecting a good adaptation to riparian habitats, which are characterised by intense and frequent disturbance events. In this context, it was surprising to observe much greater secondary biomass production in the floodplain willows when the cuttings experienced waterlogging, instead of drier conditions, prior to shoot and root removal. This was in contrast to the biomass production of the first run, where waterlogging had no effect on shoot biomass. It can be assumed that waterlogging resulted in ‘water-saturated’ cuttings, facilitating the subsequent resprouting under drier conditions, as demonstrated by Schaff *et al.* (2002), who observed the positive effect of pre-planting soaking. Under natural conditions, this could be a great advantage whenever branches or twigs, *e.g*. during flood events, fall into the water and are dispersed by the current. As soon as branches or twigs are deposited on the soil surface and moisture content decreases, water storage becomes important. The positive response to prior waterlogging occurred only in the floodplain willows, indicating that this might be another adaptation of floodplain willows to the wet–dry cycle of their habitats.

In the light of the current decline of riparian softwood forests, supporting measures are required for remaining populations and reforestations are needed (Hunter *et al.* 1999; Hughes *et al.* 2005). Comparing vulnerability and growth potential between seeds and vegetative propagules, willow reforestations are likely to be more successful when using vegetative propagules instead of seeds. However, the results of our study indicate that competition may be a factor affecting the success of reforestations to a certain degree, at least around rivers with high habitat stability and low disturbance frequency. Consequently, when plantings for restoration purposes are intended, the aboveground parts of existing vegetation should be removed at restoration sites and regular mowing should be considered as long as plantings are young. Furthermore, our results indicate that watering of floodplain willow cuttings prior to planting has positive effects on plant performance. This finding supports the recommendations of Schaff *et al.* (2002), who identified this measure as a simple, inexpensive technique to enhance planting success.

In general, reforestation using vegetative cuttings appears to be a suitable restoration measures to enhance the persistence of highly endangered riparian softwood forests along regulated rivers lacking natural recruitment (Mosner *et al.* 2011). However, sustainable regeneration of floodplain forests would require the restoration of natural river flow dynamics and geomorphological processes (*e.g.* bank erosion, channel migration, island creation), which can be summarised simply as process restoration (Beechie *et al.* 2010). These dynamics provide competition-poor, bare-ground habitats that support natural recruitment by seeds and also by vegetative reproduction units.

Acknowledgement

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Chapter 4

Managing floodplain forest restoration in European river landscapes combining ecological and flood protection issues

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Abstract

Throughout Europe the demands for improved flood protection on the one hand and the requirements to maintain and enhance floodplain forests on the other are perceived as conflicting goals in river-basin management, revealing the urgent need for strategies to combine both issues. We developed an interdisciplinary approach for floodplain-forest restoration identifying sites suitable for reforestations from both an ecological and hydraulic point of view. In the ecological module, habitat-distribution models are developed providing information on ecologically suitable sites. In the hydraulic module, a two-dimensional hydrodynamic-numerical model (2D-HN model) delivers the requested hydraulic information. The output of the two models is intersected. Subsequently, in an iterative procedure, the potential of plantings without exceeding critical water levels can be identified by hydraulic evaluation using the 2D-HN-model. The approach is exemplified using two reforestation scenarios at the Elbe River, Germany, showing considerable potential for softwood forest establishment without negative hydraulic effects.

The approach reported here provides a solution for a severe conflict in river-basin management that hampers the reestablishment of the strongly threatened floodplain forests in Europe. Alternative measures to enhance floodplain-forest regeneration feasible under certain preconditions are discussed in the context of the current state of European large rivers.

Introduction

Recent flood events across Europe—in particular the flood in the Elbe River catchment of August 2002—have caused fatalities, made thousands of people homeless, and caused damage amounting to several billion Euro (European Commission 2004). Furthermore, climate-change predictions for Europe assume that storm-generated river-flow peaks are already increasing in magnitude and frequency and are anticipated to increase in the future (IPCC 2007).

Throughout Europe, rivers and their floodplains have undergone substantial changes in the last few centuries (Petts *et al.* 1989, Tockner *et al.* 2009). These changes have been driven collectively by river regulation and fragmentation to facilitate navigation, intensifying land-use practices and increasing utilization of hydroelectric power. Of these changes the artificial narrowing of river courses, caused by the construction of dikes (also called ‘‘levees’’) to convert inundation areas into arable land, is thought to particularly amplify flood risks. In Central Europe nearly all large rivers are affected by dikes and other flood-protection measures. In Germany, a recent survey showed that only about one third of the entire floodplain area is still inundated in times of large flood events. Many stretches of the large European rivers— Danube, Rhine, Oder, and Elbe—have even lost more than 80–90 % of the former inundation areas (BMU & BfN 2009). Consequently, these floodplain areas are no longer available to retain water or alleviate flood damage. There are now major concerns about existing levels of flood defense and whether current river-basin management is adequate for preventing and mitigating the impact of future flood events.

It is often stated in the literature that forests provide natural protection from floods, and various studies have found increases in peak flows after logging although details are often the subject of great controversy (Robinson *et al.* 2003, Bradshaw *et al.* 2007). The main mechanism whereby floodplain forests are thought to aid flood defense is by slowing down the downstream passage of a flood peak, resulting in a less intense and longer lasting flood event. The delaying effect of forests on flood flows is mainly due to an increase in surface roughness. It decreases the flow velocity and simultaneously raises the water level both within and upstream of a wooded area. This backwater effect of floodplain woodlands can enhance the cumulative flood volume stored within a reach and consequently alleviate river stretches downstream (Thomas &Nisbet 2007).

However, our understanding of the influence of woodlands on floods and peak flows are far from being complete. In reviews, van Dijk *et al*. (2007) state that reforestation does not necessarily reduce flooding and Robinson *et al.* (2003) conclude that the potential for forests to reduce peak flows is much less than has often been widely claimed. Beyond that, there is severe concern that any backing-up of floodwaters could adversely affect local conditions upstream of floodplain-forest areas. The high degree of uncertainty associated with this impact has precluded any significant floodplain woodland planting to date in the United Kingdom (Thomas & Nisbeth 2007). For similar reasons plantings in inundation areas of large rivers of Germany and The Netherlands are usually discouraged. Indeed, in Germany, there have been calls to clear areas of regenerating softwood vegetation because of the potential effect of backing-up floodwaters (Dietrich 2007), and in some floodplain parts such measures have recently been conducted. Therefore, it is an important topic in European river-basin management to figure out whether and to what extent these backwater effects occur due to floodplain-forest establishment.

Apart from their unknown effects on flood peaks, riparian woodlands help foster a wide range of desirable outcomes, such as increased productivity, structural and species diversity, maintenance of water quality, water retention, and sediment and riverbank stabilization (Tockner & Stanford 2002). One subgroup of these woodlands are the so called ‘‘softwood’’ forest communities comprised of species from the family Salicaceae. Throughout much of Central Europe, deforestation for agriculture led to initial large-scale loss of riparian softwood forests. However, changed flow regimes due to dam and dike constructions are driving further declines by limiting establishment sites, reducing regeneration, and leading to over-aged populations (Brown *et al.* 1997, Tockner & Stanford 2002). Hence, riparian softwood woodlands in Europe have experienced a dramatic decline during the last few centuries (Brown *et al.* 1997, UNEP-WCMC 2000). Today, softwood forests are considered to be one of the most threatened natural ecosystems and are listed in Annex 1 of the European Habitats Directive.

The demands for improved flood protection on the one hand and the requirements to conserve the natural regeneration potential of floodplain forests on the other are perceived as conflicting goals in river-basin management and reveal the urgent need for strategies to combine both issues. In an interdisciplinary project we developed a strategy for softwood woodland reforestations by identifying suitable sites from both an ecological and hydraulic point of view. Combining two modeling techniques, the peak-flow effects of plantings at ecologically suitable sites can be assessed. From this, in an iterative procedure, reforestation sites that do not intensify flood risks by upstream backwater effects can be identified. Our aim was to provide a tool for decision makers in river-basin management in order to improve floodplain-forest restoration under observance of flood-protection issues. Alternative measures to enhance floodplain-forest regeneration feasible under certain preconditions are discussed in the context of the current state of European large rivers.

Methods

The concept is based on two modules. The ecological module utilizes habitat-distribution models for identifying sites ecologically suitable for softwood reforestations. The hydraulic module is characterized by a two-dimensional hydrodynamic-numerical (2D-HN) model. The models are merged and used in an iterative procedure to receive the requested information to arrive at the desired information on the location of sites ecologically and hydraulically suitable for reforestation purposes.

The approach is exemplified for the actively inundated floodplain (area between the dikes) of a part of the Middle Elbe River, Germany (Fig. 1), in the southeast of Wittenberge (52°56′ N, 11°50′ E, river kilometers 439–452). With a length of 1094 km and a catchment area of about 148 200 km^2 the Elbe River is one of the large rivers in Central Europe. Processes during the ice ages shaped a large glacial valley with only a small gradient in which the meandering Middle Elbe River is embedded. Sediments of the floodplain consist of permeable sands covered by a layer of alluvial loam that leads to a strong relationship between river and ground water levels (Leyer 2005). The considered river stretch has a mean annual discharge of 700 m^3 * s^{-1}. The floodplain was formerly covered by riparian softwood and hardwood forests, which were cleared for agricultural use and flood protection. Only small patches of softwood woodlands remain. These can be divided into two vegetation types, the shrubby vegetation type Salicetum triandro–viminalis Lohm., mainly containing the shrubby species *Salix triandra* L. and *S. viminalis* L., and the arboreal vegetation type, the so called Salicetum albae Issler, comprising medium-sized to tall trees of *S. alba* L. and *S. x rubens* Schrank.

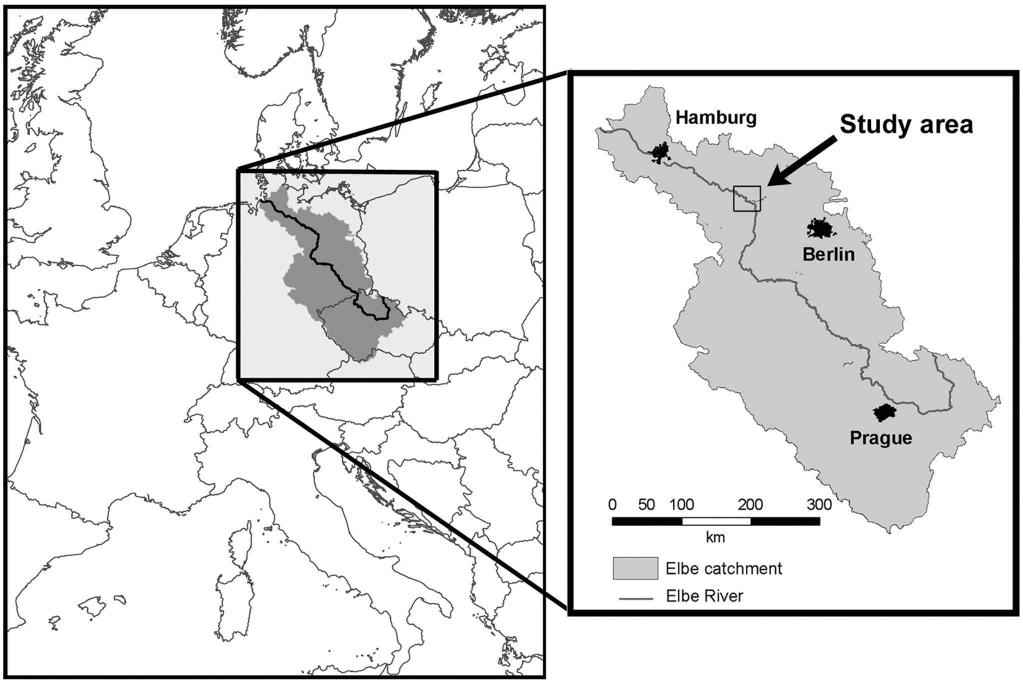

Figure 1: Location of the study area relative to the catchment of the Elbe River within Central Europe.

Ecological module

Habitat-distribution models were designed for the case study area to relate the occurrence of softwood forest species/vegetation types to hydrological variables as the most influential ecological factors of floodplain vegetation (Leyer 2005, Francis and Gurnell 2006) and methods are based on the study of Mosner et al. (2011). Results were spatially extrapolated across the floodplain to identify ecologically suitable sites for softwood-reforestation measures as input information for the further approach.

Data Sampling

Presence and absence of the two willow vegetation types (hereafter referred to as shrubs and trees) on the basis of the occurrence of the target species (*Salix triandra, S. viminalis, S. alba, S. x rubens*) were sampled in 1067 plots of 400 m^2 each during two periods in 2006 and 2007. As only remnant stands of riparian softwood woodlands were left in the study area and these were distributed across a range of environmental gradients, a stratified-randomized sampling design was employed; details are in Mosner *et al.* (2011). The sampling area comprised an Elbe River stretch of 60 km (river kilometers 415–475). The vegetation types were additionally divided into two age classes to account for niche differences of young and old vegetation. Since an exact age determination for shrubs or trees was not possible, species were indexed as ‘‘young’’ or ‘‘old’’ depending on characteristics such as stem diameter and height, degree and position of branching, and evidence of flowering.

Two hydrological variables were included as explanatory variables in the habitat model: (1) average water level (AWL), i.e., depth to the average water level (with 0 being the level of top ground surface, negative values below surface, and positive values above surface) as a measure for moisture conditions, and (2) the standard deviation of hydrographs (course of water levels over time) as a measure for water-level fluctuations (WLF). Flood duration (FD) was also calculated, but was excluded from further analyses due to high collinearity with AWL (r = 0.99). Both AWL and FD were derived from a one-dimensional (1D) hydrodynamic-numerical model (Nestmann & Büchele 2002) and a high-resolution digital elevation model (DEM; for details see Hydraulic module, below). To compute the average water level in the floodplain, the average water level of the river was extrapolated into the floodplain. Thus, AWL as well as FD in relation to the floodplain surface was calculated for each grid cell in the GIS. WLF was calculated based on the relation of river-level fluctuations and water-level fluctuations within the floodplain. Weekly water-level data from 12 piezometric head gauges (eight in front of and four behind the dike) from periods between 1989 and 2004 within the study area were transformed into continuous hydrographs. This was done by relating the river water level of the river gauge of Wittenberge as the explanatory variable to the weekly gathered water levels of each floodplain gauge as response variable by means of polynomial regression. Finally, the standard deviation as the measure for the size of fluctuations (WLF) of each time series was calculated. For details of hydrological calculations see Mosner *et al.* (2011).

Analyses

Logistic regression, i.e., generalized linear modeling (GLM) with logit link and binomial error structure was applied (Hosmer & Lemeshow 2000) to generate habitat-distribution models. This is described as a sound and simple method to predict species distribution (Guisan & Zimmermann 2000). Besides linear terms, quadratic terms for AWL were included since unimodal responses over long gradients occurred. However, WLF was always included in a linear form since only short gradients could be observed. Finally, interactions between AWL and WLF were included.

For model discrimination, we applied a threshold-free criterion, the area under the curve (AUC) of the receiver-operating curve (ROC) (Fielding & Bell 1997). Model validation was performed by a boot-strapping procedure with 1000 iterations (Guisan & Zimmermann 2000) to correct for overoptimistic estimates of performance criteria for the training data.

For a spatial extrapolation of the potential habitat in a GIS, a cutoff value for the probability of occurrence was applied to convert the values into a presence–absence data set. We chose the sensitivity-specificity equality approach (Liu *et al.* 2005). Subsequently, for the quantification of suitable habitat in the model area, the suitable habitats of the young life stages and the moist habitats of the older life stages were merged (Fig. 2). Based on field observations, they were considered to represent suitable habitats for planting material. All analyses were conducted in R (R Development Core Team 2008). The HMISC and DESIGN packages were applied for model estimation and validation (Harrell 2001).

Hydraulic module

2D-HN model

We used a high-resolution two-dimensional hydrodynamic-numerical (2D-HN) model to assess the effects of softwood forest plantings on water levels. These models are currently at the forefront of research into river flood modeling and represent a significant advancement on one-dimensional (1D) models in being able to predict smaller scale hydraulic processes, such as topographically driven floodplain flows (Beffa &Connell 2001, Nicholas & Mitchell 2003). A number of studies have shown that 2D models are capable of accurately predicting both flood extent and flood-wave travel times using independent calibration data from hydrometric and satellite sources (e.g., Horritt & Bates 2002).

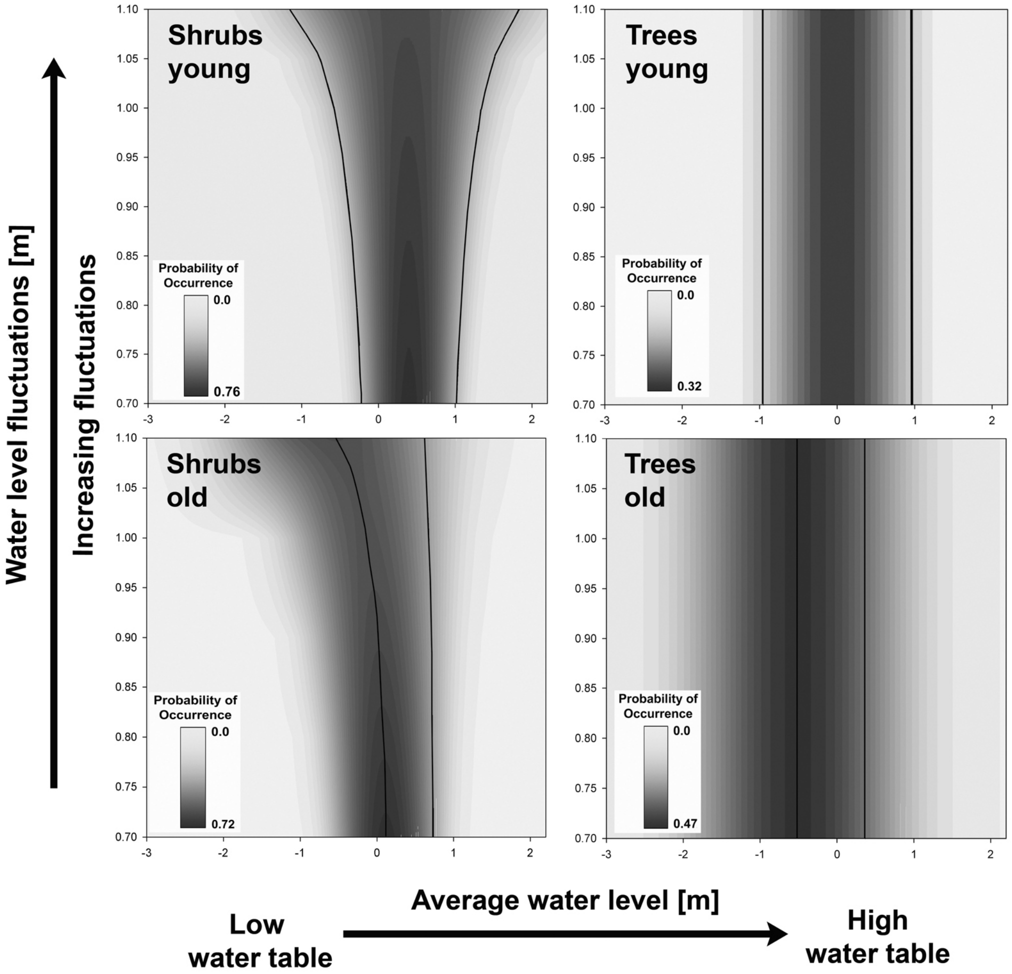

Figure 2: Contour plot of the probability of occurrence of vegetation types and age classes in relation to average water level (AWL) as a measure of moisture availability and water-level fluctuations (WLF) calculated as the standard deviation of the hydrograph. The figure is modified from Mosner *et al.* (2011: Fig. 3). Black lines: Borders of the suitable habitat for planting material.

2D models are highly sensitive to DEM inaccuracies (Horritt *et al.* 2006). Therefore, a high-resolution DEM (±0.5 m position accuracy, ±0.15 m elevation accuracy) provided by the Federal Institute of Hydrology (Germany) with the explicit integration of the riverbed geometry formed the topographical basis for the model. DEM data were derived from an airborne laser scan (lidar) conducted in 2003–2004 during mean water. Two further steps were carried out to improve the quality of the data. First, photogrammetric analyses of digital imagery information were conducted. Since respective aerial surveys were undertaken during the low-water period in August–September 2003 (this was the absolutely lowest water stage for the study area in the period 1965–2010) and ephemeral as well as many persistent water bodies ran dry, high accuracy in terms of elevations for the floodplain areas regarding oxbows, flooding channels, and depressions can be assumed. Second, concerning the river channel, data quality was enhanced based on high-resolution multi-beam bathymetry of the river bed conducted in 2004. For validation of the DEM, ground-truthing for about 2000 points was performed along cross sections of the river floodplain, resulting in a root mean-square error of 27 cm.

We used the software FLUMEN (FLUvial Modeling ENgine; Beffa 2004) providing a 2D-HN model that solves the depth-averaged shallow-water equations on a cell-centered unstructured mesh. The equations describe the flow field over moderate slopes where the pressure distribution is approximately hydrostatic. The numerical method is based on an explicit cell-centered finite volume scheme, which makes FLUMEN robust for mixed sub- and supercritical flow regimes. It is used, e.g., for flood modeling and hazard assessment; see Beffa & Connell (2001) and Beffa (2004) for more details of the model. FLUMEN reads meshes as nodes and elements. For generating a high-quality mesh for the study area the pre-processor FLUVIZ (Beffa 2004) together with the program TRIANGLE (Shewchuk 1995) was used. The triangular cell sizes of the mesh reached from 3 m^2 in high-resolution areas such as river bed, river margins, and groin structures to 1000 m^2 for some homogeneous floodplain areas. The mesh comprised altogether 116320 cells for the study area of 20.6 km^2. The calculations were based on a 100-year flood peak (extreme flood event statistically occurring every 100 years) with a discharge of 3939 $m^3 * s^{-1}$ in the studied river stretch. Results of the model available for each cell are flow velocities and water levels which were spatially visualized for our study area with the help of a GIS.

Surface roughness

The roughness of a considered area has a strong influence on water levels and flow velocities arising at a given flood peak level. Therefore, the roughness of river landscape elements (e.g., river bed, oxbows, and other floodplain water bodies, settlements, and woodlands) has to be included in the 2D-HN model to account for frictional effects. We used the roughness coefficient k_{st} according to the Gauckler-Manning-Strickler flow formula, which is one of the most commonly applied measures owing to its simplicity and the satisfactory results that have been achieved in practical applications (Chang 1988). Generally, the coefficient ranges between 1 and about 80, with higher values representing slighter hydraulic effects (Järvelä 2002). The implemented k_{st} values ($m^{1/3} * s^{-1}$) of the landscape elements in our model area (riverbed, 34; floodplain water bodies, 25; settlements, 10; and scattered shrubs and trees, 12) for the current state (without additional plantings) were figured out by model calibration. This was done by comparing observed and calculated water levels for several medium and high discharge events in the years 2001–2006. For the river bed, the values could be directly transferred from the above mentioned 1D-HN-model. The k_{st} value for potential forest plantings was based on results of laboratory experiments with both realistic flow velocities and realistic vegetation densities to obtain a reliable estimate of flow resistance caused by different softwood vegetation types and densities (Schneider 2010). Additionally, debris jams that could occur in times of large flood events within plantings should be taken into account. Therefore, in order to be on the safe side in assessing flood risks by plantings a very conservative k_{st} value of 4 $m^{1/3} * s^{-1}$ was chosen.

Results

We developed an iterative approach on the basis of the ecological and hydraulic modeling techniques in order to identify an optimum scenario. This aims to reflect the potential of plantings in a certain area without exceeding critical water levels. It comprises three main sections with a total of 10 steps.

Data input and intersection

1) Habitat-distribution models are generated as ecological input data, providing the spatial information on suitable sites for plantings (Fig. 3a).

2) 2D-HN model calculations provide the spatial information on the flow velocities for a 100-year discharge of the current state as hydraulic input data (Fig. 3b).

3) An initial flow-velocity threshold value has to be chosen to initially identify locations where floodplain velocity is low and changes in roughness are thus unlikely to influence overall floodplain hydraulics. Therefore areas depicting higher velocities than the threshold value should be excluded from reforestation.

4) In a GIS, the ecologically suitable sites are intersected with areas exceeding the threshold flow velocity (Fig. 3c).

Site selection and configuration

5) Within the remaining area suitable for plantings, sites are manually selected according to the following criteria:

   a) A minimum planting size should be ensured to guarantee that at least some of the ecological functions of forests can be provided.

   b) Sites should be selected where a conversion from grasslands to woodlands seems realistic and sites where, e.g., land use will continue in the future should be excluded.

6) A streamlined shape of each selected site is designed to minimize resistance effects in times of flood peaks (Fig. 4a).

7) A roughness coefficient (k_{st} value; see Methods: Hydraulic module: Surface roughness, above) must be assigned to the plantings to be able to assess the hydraulic effects.

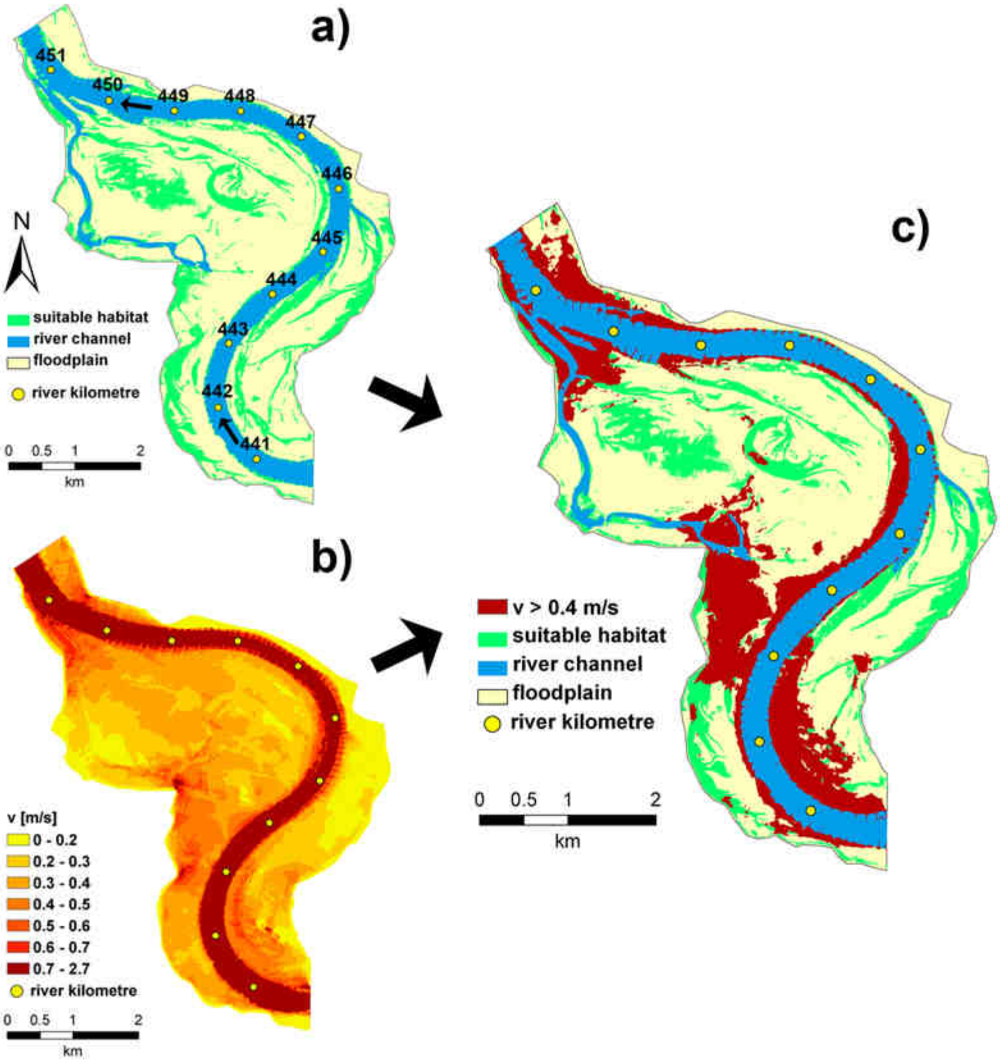

Figure 3: Input data for the iteration approach to identify suitable habitats for softwood reforestation showing the two modules separately and then the combined results. (a) Predicted habitats in the study area ecologically suitable for softwood reforestation as a result of the habitat-distribution models. (b) Flow velocities (v) for a 100-year discharge in the current-state scenario (without further plantings), calculated by the 2D-HN model. (c) Remaining ecologically suitable habitats after excluding sites with flow velocities > 0.4 m * s^{-1}.

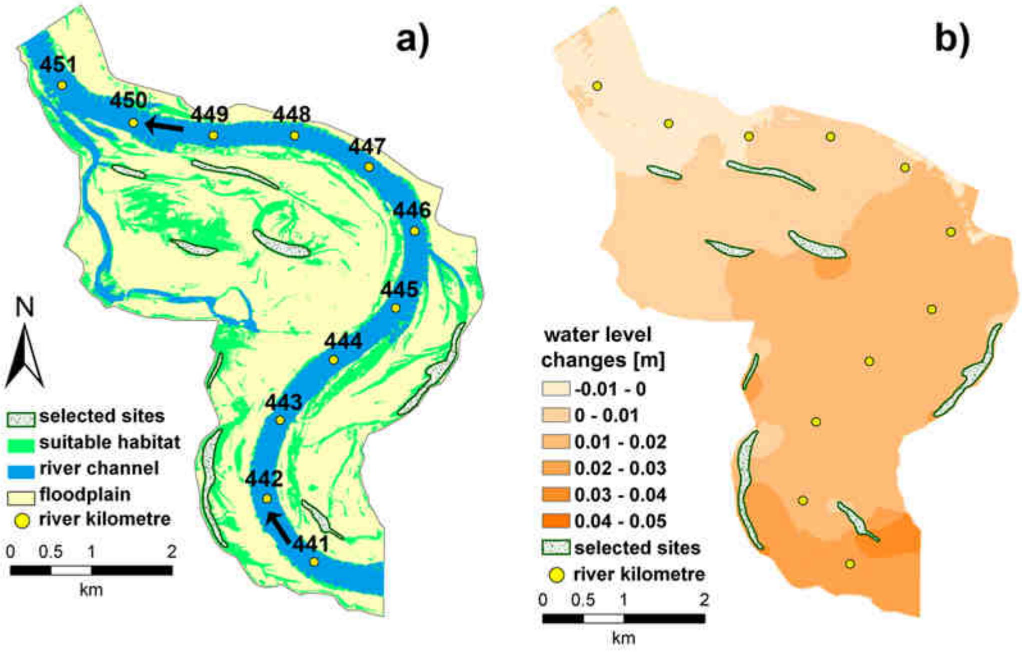

Figure 4: (a) selected planting sites summing up to a potential of ~ 49 ha additional softwood forests. (b) local water-level changes through the additional plantings compared with the current-state scenario calculated by the 2D-HN model.

Hydraulic evaluation of additional plantings

8) The water-level changes through plantings in comparison with the current state are calculated by 2D-HN modeling and visualized in a GIS (Fig. 4b).

9) Two cases can be distinguished:

Case 1. The additional plantings do not cause an intolerable increase in water levels. In this case, it can be considered to include further ecologically suitable sites even in areas with a higher flow velocity than the initially chosen threshold value. Hence, the flow-velocity thresh-old value can be raised. Subsequently, this new scenario with a higher number of sites/larger sites has to be evaluated hydraulically (steps 4–6).

Case 2. The additional plantings induce an intolerable increase in water levels, intensifying flood risks. The initial flow-velocity threshold value has to be lowered, e.g., by 0.05 m * s^{-1}, resulting in a reduction of the number and/or the size of further plantings. This new scenario similarly has to be analyzed (Steps 4–6).

10) The scenario with a maximum number and/or with a maximum area of plantings not inducing high-water risks can be identified.

Potential for softwood forest plantings in the case study area, Middle Elbe River

The approach is illustrated for the case-study area Middle Elbe River where two scenarios with five and eight planting sites of 32 and 49 ha in total size, respectively, were developed and hydraulically evaluated.

Ecological and hydraulic input data, intersection and site selection

Vegetation types as well as age classes were significantly related to the hydrological variables while their relevance changed between types and age classes (Appendix A: Table A1). Both, vegetation types and age classes were affected unimodally by AWL (average water level) with every group exhibiting a different optimum (Fig. 2). A significant interaction for shrubby vegetation was detected between AWL and WLF (water-level fluctuation), which modified the area of suitable habitat (Fig. 2). The spatial extrapolation of the models resulted in an area of 451 ha suitable for softwood reforestations with a mix of all considered species (Fig. 3a). These data represented the input information for the further approach. Two-dimensional hydrodynamic-numerical (2D-HN) modeling provided a complex view on the flow velocities during a 100-year flood peak, with large floodplain areas not exceeding a flow velocity of 0.4 m * s^{-1} (Fig. 3b). However, areas lying right in the middle of the flow path in times of floods experience strong hydraulic forces by high flow velocities. On the basis of these results we chose an initial flow velocity threshold value of 0.4 m * s^{-1}. After the intersection of ecological with hydraulic input data, 302 ha of ecologically suitable sites remained for plantings (Fig. 3c). For the first scenario, five sites with a minimum size of 1.5 ha were manually selected in a GIS, adding up to a total of 32 ha of potential planting sites (Appendix B: Fig. B1a). In the second 49-ha scenario we additionally included three sites partly in areas with a slightly higher flow velocity (Fig. 4a). For site selection, the probability of receiving permission to convert grasslands into forest played a certain role as well. Sites owned by public authorities and environmental organizations were favored in comparison to sites in private hands since the latter are generally characterized by a huge number of different owners, making it difficult to impossible to receive permission for forest plantings. Subsequently, each selected site was configured in a streamlined shape parallel to the main flow path to reduce the flow resistance of the additional plantings (Fig. 4a).

Hydraulic evaluation

The considered plantings of the 32- and 49-ha scenarios raised the flood water level to a local maximum of 3 cm (Appendix B: Fig. B1b) and 5 cm (Fig. 4b), respectively. The highest increase could be observed within and upstream of the planting sites, while downstream passages were not affected or showed a slight lowering of the flood water level. The mean change of water levels along the longitudinal course was slight in both scenarios, indicating minimal hydraulic effects of the considered forests (Fig. 5).

Discussion

The approach presented here provides a scientific basis and an application scheme for solving a severe conflict in river-basin management between nature conservation and flood protection issues. The results show that floodplain forests—placed at suitable locations—are in line with the aims of flood control. For the study area (Middle Elbe River, Germany), representing a typical European floodplain with strong hydrological alterations and intensive land use, a considerable potential for softwood-forest establishment could be determined without having significant backwater effects (i.e., the backing up of floodwaters, upstream of floodplain forest areas).

The role of softwood reforestations in riparian-forest restoration

It has to be emphasized that the sites identified as ecologically suitable for softwood reforestations cannot be equated with suitable habitats for natural recruitment. They only represent suitable planting conditions. Seedling stages could not be investigated and modeled since hardly any seedlings were detectable. Natural sexual reproduction is controlled by various factors such as the presence of competition-free, bare-ground sites, sufficient moisture in combination with suitable soil substrates, no burial by sedimentation, and no extended submersion by flooding during the growing season (Karrenberg *et al.* 2002). Therefore, in unfavorable years reproduction could be a rare event even in natural river systems (Hughes *et al.* 2000). Along European rivers, where hydro- and geomorphological dynamics are strongly constrained by dike constructions and riverbed fixations, bare-ground sites are artificially diminished to a minimum, leading to the observed lack of natural recruitment. Therefore, sustainable restoration of woodland regeneration processes would require restoration of natural river flow dynamics and geomorphological processes (e.g., bank erosion, channel migration, island creation). These can be summarized as ‘‘process restoration’’ (Beechie *et al.* 2010). However, this aim is hardly enforceable on the large scale for European river systems, which are simultaneously waterways where economic as well as social interests prevail (Buijse *et al.* 2002). To conserve the potential for such long-term aims, short-term actions such as softwood forest plantings are necessary to ensure the persistence of these vegetation types.

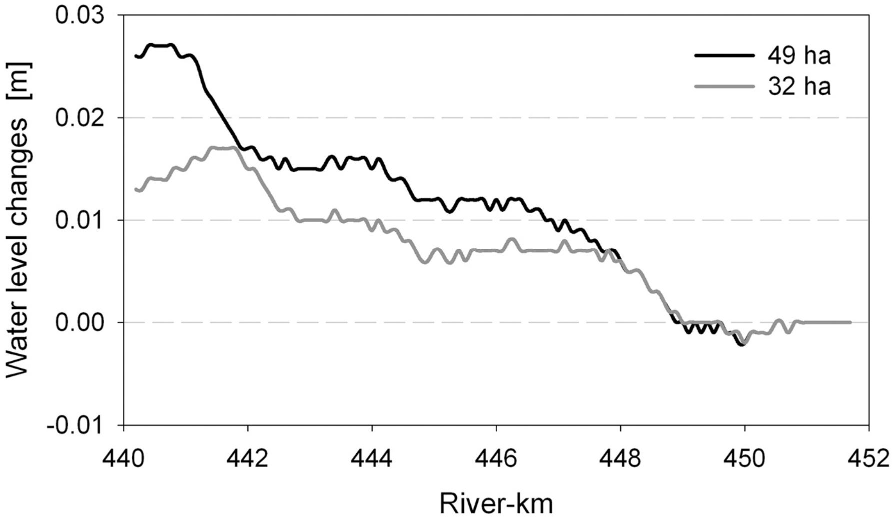

Figure 5: Mean water-level changes through the additional plantings along the considered case-study stretch of the Middle Elbe River.

Possibilities and constraints for a strategical placing of floodplain woodlands to alleviate downstream flooding

Since it has been shown, e.g., by Thomas & Nisbet (2007), that downstream passages can benefit from a backwater effect occurring within and upstream of woodlands there may be potential for using strategically placed floodplain woodlands for flood control. These measures can be appropriate in hydraulically sensitive reaches to reduce the vulnerability to floods. However, the approach presented here does not allow a quantification of downstream water-level changes associated with upstream-located forests. While the steady model utilized in our study is suitable to address the magnitude of the upstream backwater effect caused by vegetation, it is not suitable to determine the reduction in downstream peak discharge associated with this storage, which is an unsteady flow process. In the case of the modeled plantings at the Elbe River, we guess that they would not be effective for downstream discharge reduction since even locally no significant hydraulic effect could be detected. Therefore, an attenuation effect on the stretches lying farther downstream seems unlikely.

Strategically placed woodlands can only be implemented in areas where retention of a significant water volume would not increase the risk of flood damages in the vicinity of the newly created forests (Thomas & Nisbeth 2007). The implications of this factor would need to be carefully considered when assessing the suitability of individual sites for reforestations. In Germany, the implementation of such measures is additionally hampered by the fact that flood protection is under the responsibility of the federal states. Therefore, along large rivers, the costs and potential risks of forest establishment may be affiliated with one state while a different downstream-located state may profit by lowered flood peaks. On a larger scale, this mismatch arises at rivers belonging to different countries, and makes floodplain forest development difficult. Therefore, in order to improve the coordination of water and flood management we suggest organizing river-management systems and flood-defense measures as well as restoration schemes on a river-basin basis cutting across regional boundaries and national borders (European Commission 2004).

Possibilities and constraints for alternative measures to enhance the regeneration of floodplain forests under observance of flood protection issues

Recent catastrophic flood events across Europe reveal that technical solutions impeding flood damages have only limited effects and that new approaches to flood management must include the restoration of rivers' natural flood zones in order to reactivate the ability of floodplains to retain water and alleviate flood impacts (Dworak 2008). Therefore, there are tendencies in European river management to move from the traditional dike raising and reinforcement toward ''room for rivers'' measures to assure flood protection (van Stokkom *et al.* 2005). Among others, suitable measures comprise the widening of river cross sections by dike relocation, and lowering the floodplain by excavation leading to the requested increase in the water discharge capacity of the rivers. In the meanwhile, in several projects in different countries such measures are planned or already applied (e.g., Monstadt 2008). The Dutch Government has even implemented a ''room for the rivers'' concept in national management plans (van Stokkom *et al.* 2005). These kinds of measures serve both flood protection (by enlarging the retention areas) and floodplain rehabilitation (by allowing a certain dynamization of hydrological, geomorphological, and ecological processes). If they are accompanied by land-use changes from agriculture to natural development, floodplain forests can profit strongly. Floodplain lowering by excavation work, creating new pioneer stages, is a possibility in regulated floodplains lacking erosion and other disturbance processes to enhance the reoccurrence of softwood forests by natural recruitment (Friedman *et al.* 1995). However, these measures are not self-sustaining in regulated rivers either, and need continued management input to provide bare-ground sites (Rohde *et al.* 2006). Additionally, there is evidence that the initial gain in discharge capacity cannot be maintained because of the combined effect of sedimentation and vegetation succession (Geerling *et al.* 2008). Therefore, while the ecological benefit is obvious, it remains unclear where floodplain-lowering measures are suitable from a hydraulic point of view.

The most promising concept to combine the sustainable enlargement of the discharge capacity and the rehabilitation of natural processes seems to be dike relocations. Indeed, the space for such actions is limited due to the densely populated and intensively used area behind the dikes in many European regions. However, there is a certain potential for dike-relocation measures (BMU & BfN 2009) mitigating flood risks and allowing floodplain-forest development without any negative hydraulic effects as has also been stated for North American floodplain systems (Gergel *et al.* 2002). These kinds of restoration and rehabilitation projects are long-term undertakings and they need a rigorous interdisciplinary and multi-sectoral approach at all governmental, regional, and local levels (Buijse *et al.* 2002).

On the whole, there is a considerable potential to restore floodplain functions and processes while also observing and benefiting flood-protection issues. Nevertheless, due to the limited space in European river landscapes where process-inducing measures can be conducted, site-specific restoration initiatives through continued human interventions, e.g., by floodplain-forest plantings, are necessary to slow down a further deterioration of riverine landscapes and habitat diversity. The approach we have presented provides a tool for an integrated river-basin management to make floodplain-forest establishment realizable.

Acknowledgements

We thank Sandra Schneider for valuable support and discussions throughout the study, and the administration of the ‘‘Flusslandschaft Elbe Biosphere Reserve’’ for giving support whenever help was needed. We are grateful to the State Environment Agencies of Brandenburg and Saxony-Anhalt for providing groundwater data. DEM data and orthophotos were kindly provided by the Federal Waterways Engineering and Research Institute and the Federal Institute of Hydrology. We thank two anonymous reviewers for valuable comments on an earlier version of this manuscript and Jarrod Kath for his kind help improving the English of the manuscript. This study was funded by the Deutsche Bundesstiftung Umwelt (DBU-AZ 23649).

Appendix

Table A1: AUC values as indicators of model performance and final model structure regarding hydrological variables of the two vegetation types and the two age classes.

Vegetation Group	AUC (Training/Evaluation)	Final model structure
Trees old	0.736 / 0.733	~ AWL + AWL^2
Trees young	0.898 / 0.892	~ AWL + AWL^2
Shrubs old	0.873 / 0.870	~ AWL + AWL^2+WLF+AWL^2*WLF
Shrubs young	0.922 / 0.918	~ AWL + AWL^2+WLF+AWL^2*WLF

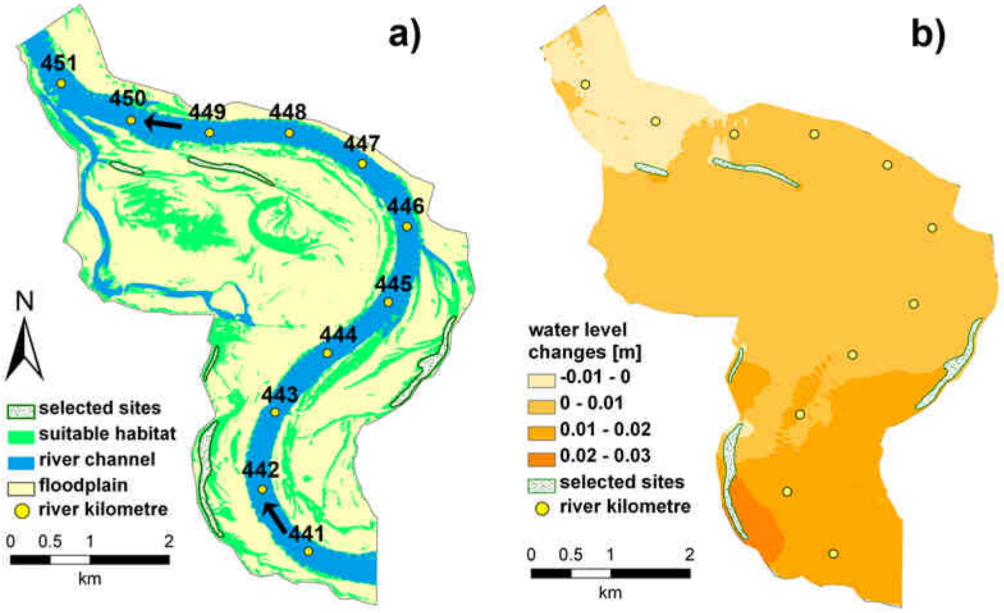

Figure B1: (a) selected planting sites summing up to a potential of approximately 32 ha additional softwood forests. (b) local water-level changes through plantings compared with the current state scenario calculated by the 2D-HN model.

Chapter 5

Azonal vegetation under climate change: Riparian softwood forest responses to climate-driven hydrological changes

Eva Mosner, Tobias Conradt, Fred Hattermann & Ilona Leyer

Manuscript

Abstract

Azonal vegetation like riparian forests is characterised by its uniformity across different regional climate zones and distribution depends mainly on local soil moisture conditions. Therefore, studies on climate-induced changes in riparian species' distribution should not focus on macro-climatic but on hydrological factors, which are the most influencing variables. However, little quantitative information on the potential changes in the extent and distribution of riparian vegetation as a consequence of climate change is available. Therefore, we estimated changes in the small-scale distribution of riparian softwood forest habitats based on climate-driven hydrological alterations along a Central European river stretch utilising a combination of a spatial eco-hydrological model and habitat distribution models. Different realisations of the river discharge produced by the hydrological model, divided into high, middle and low realisations of two future periods, were used to derive future conditions. Although the results revealed a great variability in future habitat distribution, many realisations, especially those of the far future, indicated habitat reductions for both vegetation types and age classes, with the trees being more severely affected than the shrubs. In order to improve the success of forest restoration activities we identified sites suitable for restoration plantings under current as well as future conditions by intersecting suitable habitats of all realisations. Riverbanks, floodplain depressions, and oxbow lakes were identified as most suitable. Possibilities to restore these morphological structures as well as to mitigate further deterioration of riparian forests are discussed.

Introduction

Riparian softwood forests comprising different tree and shrub species of the Salicaceae family are a major vegetation type of floodplains throughout the northern hemisphere. In Europe, these forests belong to the most endangered habitat types according to the EU Habitats Directive (92/43/EEC 1992). The UNEP World Conservation Monitoring Center (2000) estimates that 99.5% of the continental, alluvial willow forests in Europe have been lost. Major threats to these forest communities are river regulation by dam construction for navigation, irrigation and power production purposes as well as floodplain fragmentation by dykes (also called levees) which caused an enormous loss of floodplain areas (Nilsson *et al.* 2000; Tockner *et al.* 2002). In the remaining, actively inundated floodplain softwood forests were widely cleared for agricultural usage. Moreover, as a consequence of the various river engineering measures, intensive hydro- and morphodynamics leading to bare ground habitats suitable for seedling establishment are severely restricted and thus natural recruitment of these pioneer species is almost absent in many European rivers (Hughes *et al.* 2001). Therefore, sustainable floodplain forest restoration would require restoration of natural river flow dynamics and geomorphological processes, which is mostly not accomplishable in the densely populated European river landscapes where rivers are simultaneously waterways with great economic and social importance (Leyer *et al.* in press). Therefore, site-specific restoration initiatives by floodplain forest plantings are necessary to prevent further reductions of floodplain forests (Winfield *et al.* 2002; Hughes *et al.* 2005)

Climate change represents another hazard for the persistence and functioning of floodplain ecosystems (Palmer *et al.* 2008; Erwin 2009; Palmer *et al.* 2009) and fundamental effects on floodplain biota and on floodplain vegetation in particular are expected (Lite *et al.* 2005; Ström *et al.* 2011). Generally, climate change effects on the distribution of species are assessed by focusing on variables reflecting macroclimatic conditions such as temperature and precipitation (Walther *et al.* 2002; Thuiller *et al.* 2005; Pompe *et al.* 2008). This approach is suitable for zonal vegetation, which responds mainly to macro-climatic factors. However, azonal vegetation types such as floodplain, coastal, bog or fen vegetation is surely captured suboptimally with such an approach (Watson *et al.* 2009; Talbot *et al.* 2010). Such vegetation types occur across a wide range of different climate zones, with local edaphic conditions (e.g.

soil moisture, soil salinity) being the major driver for their regional and local distribution (Breckle 2002). Consequently, studies linking riparian vegetation distribution to climate change should be conducted at smaller spatial scales and they must include hydrological variables as the most influential factors structuring floodplain vegetation. This is of great importance as hydrology of rivers and adjacent floodplains will most likely change in the future (Hattermann *et al.* 2007; Palmer *et al.* 2008; Görgen *et al.* 2010). Unfortunately, little quantitative information on potential changes in hydrological conditions of European rivers is available and even less concerning the potential changes in the extent and distribution of riparian vegetation as a consequence of climate change.

Regarding riparian softwood forests, potential changes might not only entail problems for existing stands. Also, the success of reforestation measures could be severely compromised if sites currently suitable for restoration plantings will loose their suitability due to climate change. Hence, the effects of climate-change driven hydrological alterations on the distribution of vegetation habitats need to be assessed to effectively apply conservation measures for this forest type.

Therefore, in the present study, we estimated changes in the small-scale distribution of riparian softwood forest habitats in relation to climate-driven hydrological alterations along a Central European river stretch based on a spatially semi-distributed eco-hydrological model and habitat distribution models. The aim was to assess the potential impacts of future hydrological changes on riparian forests and to identify sites currently and in future suitable for floodplain forest plantings in order to enhance the success of floodplain forest restoration.

Methods

Study area and species

The study area comprises a 60 km stretch along the lowland part of the Elbe River, in the vicinity of Wittenberge (52° 59.5’ N, 11° 45.0’ E, Appendix Fig. A.1). The Elbe River is one of the largest rivers of Central Europe with a catchment area of 148 242 km^2 and a total length of 1 094 km. The river stretch is characterized by an annual average discharge of about 700 m^3 * s^{-1}, with strong seasonal water level fluctuations. Highest water levels commonly occur in spring with the lowest in autumn. Sediments of the river floodplain are characterized by highly permeable sands covered by a layer of alluvial clay. As a consequence, there is a strong relationship between river and ground water levels in the floodplain (Schwartz *et al.* 2003; Leyer 2005). Dyking of the river has reduced the area of the active floodplain by about 90 % (BMU & BfN 2009). Riparian softwood and hardwood forests, which formerly covered large parts of the active floodplain, were widely cleared for agricultural use and only small patches of softwood woodland remain. The softwood forest communities of the study area comprise two vegetation types: the shrubby vegetation type Salicetum triandro-viminalis Lohmeyer with the dominant species *Salix triandra* and *S. viminalis*, and the arboreal vegetation type, the so called Salicetum albae Issler, characterized by medium-sized to tall trees of *S. alba*, *S. × rubens* Schrank and *Populus nigra*.

Sampling design, species data, and abiotic predictors

Data collection and habitat distribution models used in this study are described in detail in Mosner *et al*. (2011). In the following, we summarise these methods. Species distribution data were sampled during 2006 and 2007. Sampling was based on a stratified-randomized design covering an elevation gradient as well as a distance-to-river gradient.

In each of altogether 1067 sampled plots of 400 m^2, the presence/absence of the four target species, *S. alba*, *S. × rubens, S. viminalis,* and *S. triandra* with one randomly selected individual per species and its precise position was recorded using a DGPS (with deviation < 1 m) . Individuals of each species were classified into two age classes, “young” or “old” based on morphological characteristics such as diameter at breast height, height and branching pattern. For subsequent analyses, species data were pooled into vegetation types combining *S. alba* and *S. × rubens* to the tree type and *S. triandra* and *S. viminalis* to the shrub type.

The distribution pattern of riparian vegetation and more specifically softwood forest species at the river reach scale is mainly influenced by hydrological variables (Leyer 2005; Francis *et al.* 2006). Hence, two hydrological variables accounting for the elevational and distance-to-river gradient were used to model the current species habitat:

1. Average water level (AWL) relative to the ground surface, with negative values indicating a relative position of the water table below ground surface and positive values denoting a relative position above.

2. The standard deviation of water level hydrographs, which represents water level fluctuations (WLF) declining with the distance to the river.

Calculation of the AWL was based on a 1-dimensional hydrodynamic-numerical model (Nestmann & Büchele 2002) and a high resolution Digital Elevation Model (DEM). The DEM data (2 m spatial resolution, ±0.5 m position accuracy, ±0.15 m elevation accuracy) were derived from an airborne laser scan (LiDAR) conducted in 2003/2004 during average flows. To further improve quality of the data, photogrammetric analyses of digital imagery information of the low water period in August/September 2003 was conducted. For validation of the DEM, ground truthing for about 2000 points was performed resulting in a root mean square error of 27 cm.

The reference level for AWL calculations was based on the annual average discharge measured at the river gauge Wittenberge for the reference period 1995 – 2005, i.e. 665 $m^{3*} * s^{-1}$. The sediments of the floodplain consist of permeable sands covered by a layer of alluvial loam that leads to a strong relationship between river and ground water levels. Therefore, to compute the AWL across the floodplain, the reference level could be extrapolated into the floodplain. Using a Geographical Information System (GIS), the AWL was calculated and converted to a raster map with a resolution of 2 m.

Water level fluctuations were calculated based on the relationship between river level fluctuations, water level fluctuations within the floodplain, and distance to the river. Weekly groundwater level data (period 1989–2004) of eight piezometric head gauges in the floodplain were analyzed using polynomial regression with the river water level of the river gauge at Wittenberge as the explanatory variable. To account for delays and dampened fluctuations of the groundwater table, moving averages and time lags were applied to the hydrograph of the river water level. The resulting polynomial functions of each groundwater level were subsequently applied to the time series of the river level for the period 1995–2005 (Fig. 1).

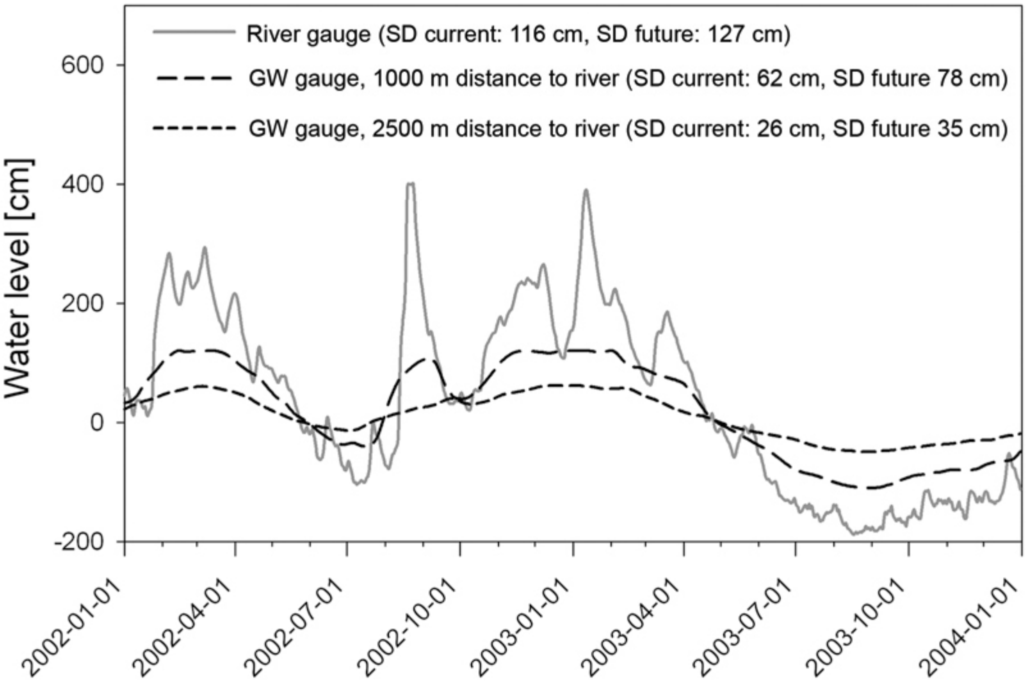

Figure 1: Relation of river water level and ground water levels measured at two groundwater gauges in the Elbe River floodplain in different distances to the river. In parentheses, the standard deviation of the hydrographs for the current (1995 – 2005) and future period (average for the 15 realisation runs for the two future periods, 2023 – 2033 and 2043 – 2053) is given.

For each continuous hydrograph of the piezometric head gauges the standard deviation (SD) as a measure of water level fluctuations was calculated. To obtain spatial information on WLF, the standard deviation of the eight groundwater gauges and the river water level were tested against the distance to the river applying different models (linear, quadratic and asymptotic) and the best model (asymptotic) was applied to interpolate WLF across the floodplain (Appendix Fig. A.2).

Habitat distribution models

Generalized linear models (GLM) with logit link and binomial error structure were used with presence-absence data of the vegetation types as the response variable and hydrologic variables as the predictors (Hosmer and Lemeshow 2000). Variable selection was conducted by a stepwise backwards selection with an exclusion criterion of $p < 0.05$. Model selection was based on the Likelihood-Ratio-Test (Hosmer & Lemeshow 2000). In the case of AWL, quadratic terms were included to account for unimodal responses, while WLF were only incorporated in a linear form. Interactions between AWL and WLF were also tested for.

Predictive power of the models was evaluated using a threshold-free criterion, the area under the receiver-operating characteristic curve (AUC). Model performance was assessed according to Hosmer & Lemeshow (2000; acceptable: AUC > 0.7, good: AUC > 0.8, excellent: AUC > 0.9). Validation of the models was conducted on the basis of an evaluation data set, which was produced by a bootstrapping procedure with 1000 iterations (Guisan and Zimmermann 2000). To compare current with future habitat distribution, a cut-off was applied to the probability of occurrence in order to convert the probability values into a presence–absence dataset. We chose the sensitivity–specificity equality approach (Liu and others 2005). All analyses were conducted in R (R Development Core Team 2008). The HMISC and DESIGN packages were utilised for model estimation and validation (Harrell 2001).

Climate change scenarios and habitat distribution model projections

Climate change scenarios of hydrological variables for the Elbe River basin were based on the study of Hattermann *et al.* (2007). As the baseline scenario the IPCC SRES A1B (Intergovernmental Panel on Climate Change Special Report on Emission Scenarios, IPCC 2007) was used. In combination with the global circulation model ECHAM4 (Roeckner *et al.* 1996) a temperature trend of about 1.4 K increase until 2055 for Germany was produced. This trend built the boundary conditions for the regional climate model STAR (STAtistical Regional model; Orlowsky *et al.* 2008). For the period 2004 – 2055, 100 time series of weather conditions for the Elbe River basin were calculated reflecting the temperature trend for this period and the observed climate pattern for the region (Orlowsky *et al.* 2008). The 100 climate change realisations produced by STAR displayed the meteorological boundary conditions as drivers for 100 realisations of the river discharge calculated by the spatially semi-distributed eco-hydrological model SWIM (Soil and Water Integrated Model; Krysanova *et al.* 1998). This model is based on components of two previously developed models, SWAT (Arnold *et al.* 1993) and MATSULU (Krysanova *et al.* 1989). SWIM integrates hydrology, vegetation, erosion, and nitrogen dynamics at the watershed scale. It is spatially disaggregated into three levels, comprising the basin scale, sub-basins, and hydrotopes at the lowest level (i.e. areas of homogenous hydrologic response as related to land use, soil types, and weather conditions). Regarding the Elbe River catchment, overall more than 45 000 hydrotopes and 2 278 sub-basins were modelled. For the hydrological module of SWIM necessary weather input variables are daily precipitation, air temperature (average, minimum, maximum) and solar radiation. These are the basis to model time series of water fluxes separately for each hydrotope (for details see Krysanova *et al.* 1998). Subsequently, all discharge components are calculated for each hydrotope and aggregated at the sub-basin scale. Finally, sub-basin outputs are added and routed according to the river system structure to derive river discharge simulations for the main river gauges.

In order to test the effects of climate-induced changes in hydrology on softwood forest communities, hydrological variables, i.e. future AWL and WLF were calculated based on the future daily discharges of the river gauge of Wittenberge. Two 10-year periods of future discharges were extracted from the whole time series for comparison with the reference period 1995-2005. These are the periods 2023 – 2033 and 2043 – 2053, hereafter referred to the 2023 and 2043 period, respectively. Subsequently, all 100 realisations of both periods were divided into low, middle and high discharge realisations (hereafter referred to discharge groups) by dividing the range of the highest and the lowest average discharge into three equal intervals. Subsequently, five realisations per discharge group for each period (= 30 realisations) were randomly selected as the basis for climate change projections of softwood forest habitats.

Time series of the future discharge of the gauge Wittenberge were transformed into water level hydrographs (Fig. 2) based on its stage-discharge relation to extract the necessary information on average water levels (AWL) and water level fluctuations (WLF). In comparison to the reference period, computed future AWL resulted in average changes of + 12 cm, -22 cm, and –47 cm for the high, middle, and low discharge groups for the 2023 period, respectively and in –18 cm, -57 cm, and –95 cm for the 2043 period, respectively (Fig. 3a). Changes correspond to a mean of average discharges in the 2023 period of 105%, 91% and 79% in relation to the reference period for the high, middle and low discharge groups, respectively and in the 2043 period 92%, 77% and 62%, respectively. Average water levels were extrapolated into the floodplain as described above.

To deduce WLF, hydrographs for the groundwater gauges were calculated based on the hydrographs of the river water level for the 15 realisations per period and the polynomial functions, which were previously calculated based on the measured groundwater data. Subsequently, the standard deviation of all hydrographs as the measure for WLF was computed. Differences in WLF among the altogether six discharge groups of both periods were tested by an ANCOVA with log-transformed WLF as the response variable, the distance to the river as the continuous predictor variable and all discharge groups of both periods as the factorial predictor. Since no differences in model response for the different groups could be detected (Fig. 3b, Appendix Table A.1), WLF of the six discharge groups were treated as one group to calculate a final model of WLF against distance to the river, based on an asymptotic model analogously to the asymptotic model of the reference period (Appendix Fig. A.2). This model was used to extrapolate future WLF as a function of distance to the river across the floodplain. Overall, WLF increased for the future projections with slight increases close to the river and more pronounced differences further away (Appendix Fig. A.2).

Finally, climate change projections of AWL and WLF were used as abiotic predictor variables in the habitat distribution models to compute habitat suitability for the different life stages of the two vegetation types under future conditions. Subsequently, model comparison of current and predicted habitat was carried out by intersecting future projections with the reference state in a GIS. For this, the occurrence probabilities of each projection were transformed into presence–absence data according to Liu *et al.* (2005, see above). We compared current and future distributions of the habitat for each vegetation type and age class summing up the grid cells of potentially lost, gained, and stable habitat.

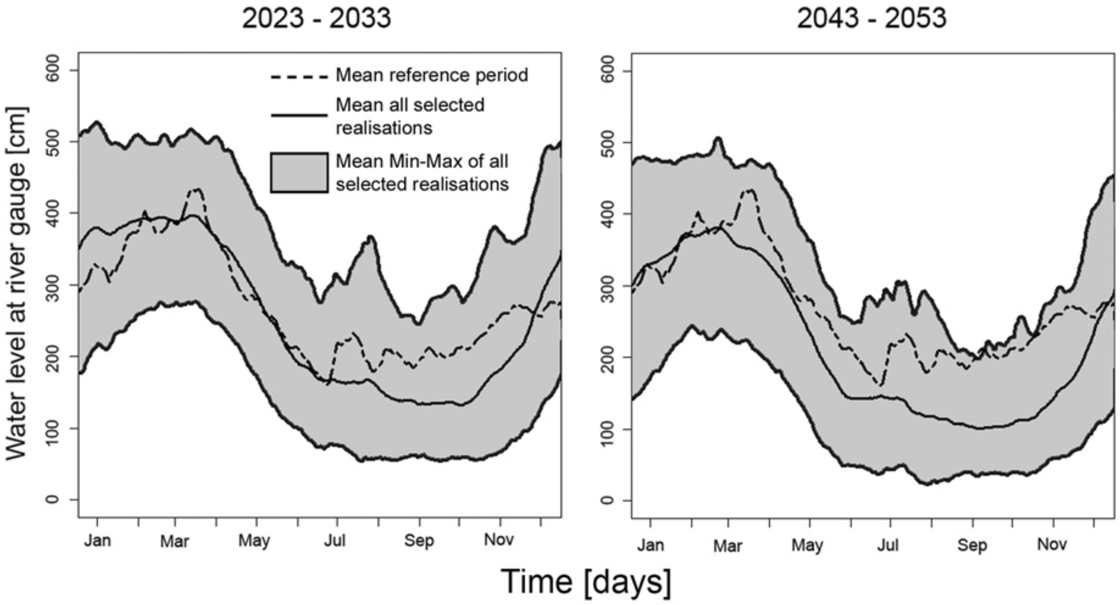

Figure 2: Average daily water levels of the river gauge Wittenberge for the reference period (1995 – 2005; dashed line) and for the 15 selected realisations of each future period (2023 – 2033, left; 2043 – 2053, right). For the future periods the mean of all average daily water levels (solid line) is given as well as the mean of the minimum/maximum of all realisations.

Identification of sites suitable for restoration plantings

Habitats of young vegetation (shrubs and trees) are considered as suitable sites for restoration plantings by vegetative cuttings (Mosner *et al.* 2011). Regarding the large variability in future discharges detected for the different realisations it is reasonable to identify those sites which are suitable for restoration plantings, now and in the future under all discharge realisations in order to improve the success of floodplain forest restoration measures. Therefore, the following approach was conducted: First, the five realisations of each discharge group were summarized by keeping presences of the projected habitat of young shrubs and trees only if all five projections predicted the presence of the habitat (Araujo *et al.* 2007). Afterwards, the results were summarized for all three discharge groups of one period to receive the minimum amount of suitable habitat available under the whole range of potential future conditions. Suitable planting sites under current and future conditions were identified by intersecting habitats using a GIS. To identify potential restoration sites suitable for plantings over the whole time, i.e. under current and future conditions of both periods, firstly the reference period with the 2023 period and subsequently the 2023 with the 2043 period was intersected.

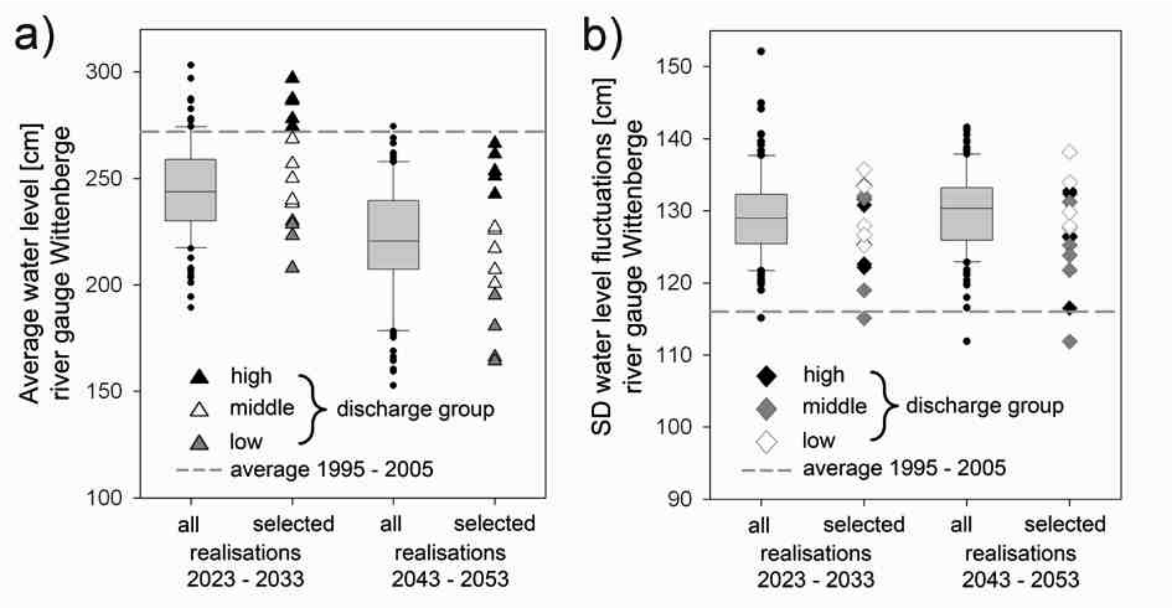

Figure 3: a) Average water levels and b) standard deviations (SD) of water level fluctuations of all 100 realisations (boxplots) as well as of the 15 selected realisations distinguished for the discharge groups (low, middle and high) and the two time periods (2023 – 2033 and 2043-2053). Dashed lines indicate conditions of the reference period (1995 – 2005).

Results

Habitat distribution models of the vegetation types and age classes performed well (AUC training/evaluation: old trees: 0.736/0.733, young trees: 0.898/0.892; old shrubs: 0.873/0.870; young shrubs: 0.922/0.918). Both young and old trees showed only significant relations to AWL. In contrast, habitat distribution for both shrub groups was also determined by the interaction of AWL and WLF. Under high WLF (near the river), the shrub habitats were enlarged along the AWL (and thus elevation) gradient in comparison with sites of more stable water tables (Fig. 4). Old shrub habitats occupied additional sites of higher elevations whereas young shrub habitats were expanded to both higher and lower located sites.

Habitat distribution projections

Habitat distribution projections revealed great differences between discharge groups and simulation periods (Table 1). Regarding the “2023 high discharge”-realisations, habitat loss was negligible for both vegetation types and age classes not exceeding 10.2 %. In contrast, the amount of lost habitat increased rapidly in the other two 2023 discharge groups up to 53 % under the low discharge-realisations for the young trees. A similar pattern was observable for the 2043 period with even larger habitat losses.

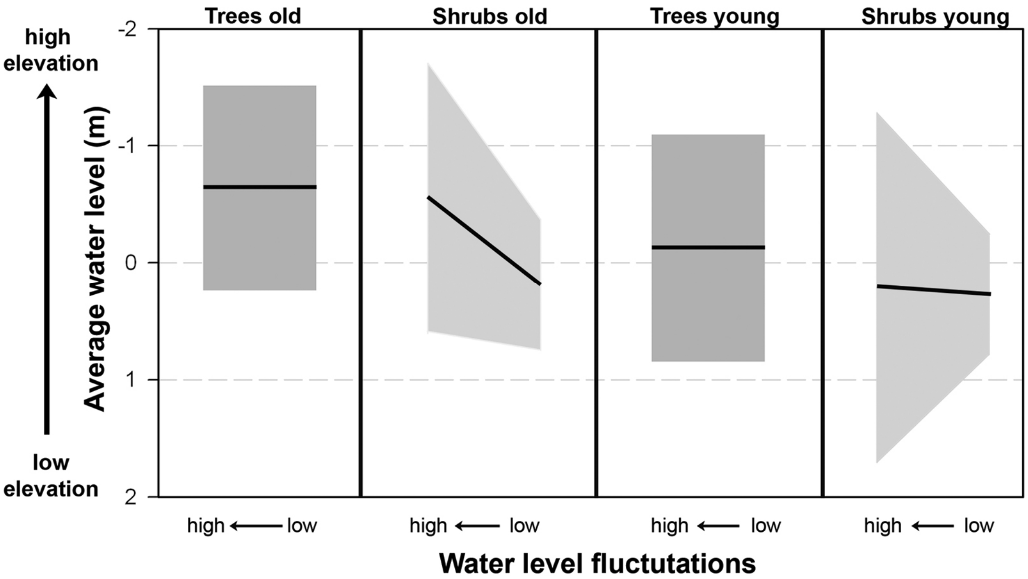

Figure 4: Vegetation type and age class responses in relation to the average water level and water level fluctuations. Grey polygons denote suitable habitat in relation to the two hydrological gradients, black lines indicate the habitat optima.

Habitat gains could compensate for habitat losses in the case of the shrubs regarding the high and middle discharge groups of the 2023 period and the high discharge group of the

2043 period. In the case of the trees the gain exceeded loss in the high discharge group of the 2023 period (Table 1). Overall, relative habitat gains were much larger for the shrubs than for the trees and likewise losses were mostly smaller (Table 1).

Summarizing habitat gains and losses, for the tree vegetation, changes in availability of future habitat in relation to the current habitat was only negligible in terms of the high discharge realisations of the near future period (Fig. 5a). Under all other groups, decreases in habitat availability were pronounced. With around 30 - 40 % habitat available for both tree life stages the low discharge realisations of the far future exhibited the absolute minimum of all scenarios (Fig. 5b). Concerning the two life stages of shrubs, future habitat availability equalled or even exceeded the current habitat availability for the middle and high discharge realisations of the 2023 future period and the high discharge realisations of the 2043 future period. However, similarly to the tree species, future habitat availability declined for the other groups to a minimum of about 60 – 75 % of the current available habitat (Fig. 5b).

Identification of suitable planting sites considering future hydrological conditions

Assessment of suitable reforestation sites based on the habitat of young trees and shrubs revealed that only little area remained suitable for restoration plantings in the near future and further decreased towards the far future (Table 2, Fig. 6, Appendix Fig. A.3). However, considerable differences between tree and shrub habitat were identified. In general, more area remained as suitable planting sites in terms of the shrub habitats when summarising all discharge groups for both periods. For both vegetation types, negative changes in the near future were more pronounced than during the far future. Relating the amount of planting habitat suitable under the whole range of possible future conditions until 2043 to the currently available habitat, only about 13.5 % for the trees was left (Fig. 6). For the young shrubs, this amounted to about 39.4 % (Appendix Fig. A.3).

Table 1: Percentage of habitat gains and losses in relation to the current habitat for the two simulation periods 2023 and 2043 for the different vegetation types and age classes for the whole the study area.

Vegetation type	Period	Discharge group	Gain (%)		Loss (%)	
			Mean	Range	Mean	Range
Trees old	2023	high	10.4	2.6 – 21.0	2.8	0.6 – 6.2
	-	middle	3.3	0.8 – 5.5	19.0	3.4 – 34.1
	2033	low	7.2	6.0 – 9.9	46.4	37.4 – 66.1
	2043	high	3.0	1.4 – 4.5	16.8	10.7 – 26.6
	-	middle	7.9	5.6 – 9.9	51.5	34.9 – 66.1
	2053	low	13.1	11.3 – 15.2	79.9	73.4 – 86.5
Shrubs old	2023	high	45.0	31.9 – 61.7	4.1	2.8 – 6.5
	-	middle	28.9	15.4 – 28.5	11.3	3.1 – 20.6
	2033	low	15.5	14.3 – 18.9	31.3	23.1 – 52.0
	2043	high	21.4	17.2 – 25.9	9.1	4.3 – 15.3
	-	middle	16.0	14.3 – 18.9	36.7	21.2 – 52.0
	2053	low	29.0	23.2 – 34.8	68.0	60.5 – 75.4
Trees young	2023	high	14.7	3.5 – 30.5	1.8	0.4 – 3.8
	-	middle	3.2	0.6 – 5.7	23.8	4.6 – 41.4
	2033	low	8.8	6.4 – 15.1	52.8	44.8 – 69.7
	2043	high	2.5	0.6 – 4.4	19.5	4.6 – 33.1
	-	middle	10.1	5.9 – 15.1	57.3	42.3 – 69.7
	2053	low	21.8	18.3 – 25.6	81.7	75.7 – 87.6
Shrubs young	2023	high	40.4	30.6 – 54.8	10.2	8.2 – 13.0
	-	middle	20.2	17.8 – 25.3	14.0	7.9 – 21.8
	2033	low	20.8	18.8 – 25.7	31.3	24.2 – 46.9
	2043	high	19.0	17.1 – 20.7	12.1	8.5 – 17.0
	-	middle	22.1	18.3 – 25.7	35.5	22.4 – 46.9
	2053	low	31.1	28.1 – 34.5	57.7	52.5 – 63.1

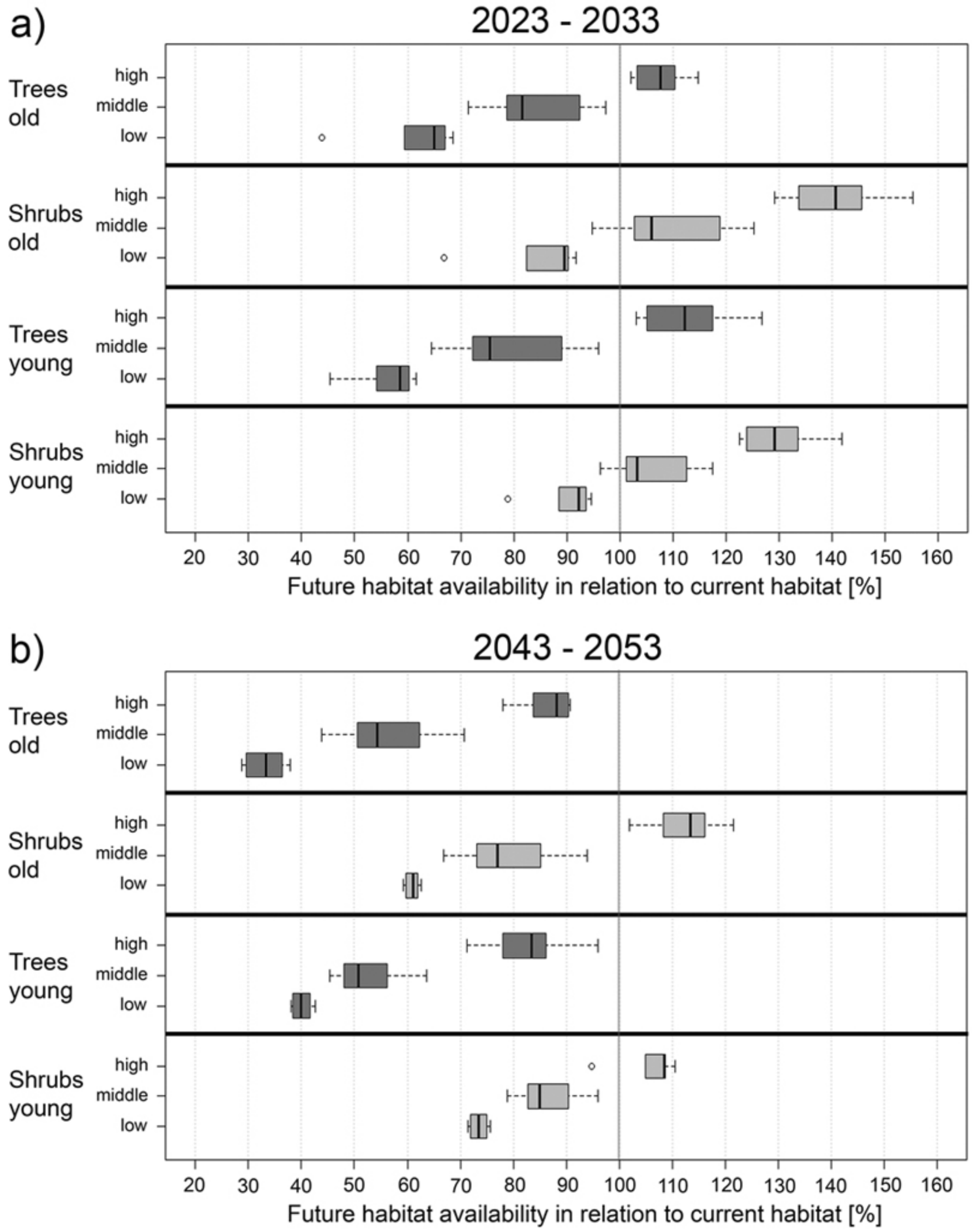

Figure 5: Boxplots of the relative amount of future habitat in relation to current habitat of the reference period for tree and shrub vegetation for both age classes in relation to the three different discharge groups (low, middle, high) for both future periods (5a: 2023 – 2033 and 5b: 2043 – 2053).

Discussion

Our study revealed that there is considerable variation in projections regarding the availability of suitable habitat for riparian softwood forests. Possible changes reached from notable increases in suitable habitat to serious decreases depending on the investigated vegetation types and the discharge realisations. Given the fact that only one model chain was applied for projections and only one hydrologic model was used to transform macro-climatic changes into hydrologic alterations, defining future habitat availability for riparian softwood forests appears to be difficult. However, our results provide a first assessment of the range of possible consequences for riparian softwood forests in relation to the most influencing, i.e. hydrological, variables determining the availability of suitable habitat for these species. So far, modelling studies assessing possible climate change effects mostly analysed potential range changes of species in relation to macro-climatic variables (e.g. Thuiller *et al.* 2005; Araujo *et al.* 2011). Pompe *et al.* (2008) used, amongst others, a climate change scenario comparable to ours to project the distribution of 845 European plant species for Germany based on macro-climatic variables. The results revealed large effects on many species. However, little evidence was found for negative impacts on the distribution of the three softwood forest species *S. alba, S. triandra,* and *S. viminalis* for the investigated river stretch (Kühn, I., personal communication). This is not surprising since riparian *Salix* species are able to grow under a wide range of climatic conditions. They are widely distributed throughout the Northern hemisphere, occurring from temperate to Mediterranean climates in Central and Southern Europe, respectively and to steppe climate in Central and Eastern Siberia (Skvortsov 1999). Furthermore, they have successfully invaded similar climatic regions throughout the Southern hemisphere such as areas along Patagonian rivers (Budde *et al.* 2011) as well as floodplains in South-East Australia and South-Africa (Henderson 1992; Adair *et al.* 2006). Consequently, macro-climatic factors restrict distributions of such species only to a minor degree and therefore, the inclusion of the small-scale drivers of azonal vegetation for sure greatly improves the quality of models and projections.

Differences in tree and shrub responses to hydrological changes

The results revealed that tree habitats were more negatively affected by projected hydrological changes than shrub habitats. Tree habitats showed fundamental losses especially for stronger AWL changes. Habitat gains occurred only along oxbow lakes, in flood channels, depressions, and along the riverbanks which were characterised by aquatic conditions unsuitable for softwood woodlands afore. As these morphological structures are heavily restricted in number and size within the floodplain, habitat losses outweighed gains in the case of the softwood tree vegetation. In contrast, shrub habitats displayed pronounced losses also, but habitat gains were much larger compared to the trees. At first glance this phenomenon seems surprising since shrub vegetation was clearly related to AWL and projected AWL changes affected softwood shrubs negatively. However, the positive effect of an increase in water level fluctuations has to be taken into account. It is a result of the wider elevational niche that can be occupied by the shrubs when water level fluctuations are high enough to recurrently wet the soil of sites of higher elevations and to provide a terrestrial phase in low lying depressions which are otherwise permanently under water (Leyer 2005; Mosner *et al.* 2011).

Table 2: Percentage of stable, gained, and lost area of suitable planting sites for the two different vegetation types for the whole study area. Displayed are relations of currently available sites to 2023 period conditions (indexed with a) and relations of sites available for the 2023 period to 2043 period conditions (indexed with b).

Vegetation type	Future period	Stable planting sites [%]	Gained planting sites [%]	Lost planting sites [%]
Trees	2023-2033	26.6^{a}	0.0^{a}	73.4^{a}
	2043-2053	32.4^{b}	18.6^{b}	67.6^{b}
Shrubs	2023-2033	40.6^{a}	2.5^{a}	59.4^{a}
	2043-2053	57.5^{b}	33.8^{b}	36.6^{b}

Consequently, increased WLF as predicted for the future led to an increased amount of suitable shrub habitat. However, with further decreasing AWL this phenomenon was obscured. Increased losses of suitable habitat and gains primarily occurring in groyne fields along river banks led to a severe habitat reduction in most of the far-future projections.

Implications of hydrological change effects on the different life stages

Patterns of habitat losses and gains were similar for the different life stages within each vegetation type, yet their relevance is likely to differ. With regard to the older life stages, habitat loss resulting from unsuitable growing conditions in the future due to decreased water availability could lead to accelerated rates of stand dieback of extant old vegetation (Lite *et al.* 2005; Rood *et al.* 2008; Gonzalez *et al.* 2010b). Moreover, these sites could exhibit suitable growing conditions for riparian hardwood forest species, which are adapted to dryer conditions. Thus, old riparian softwood vegetation could suffer from drought stress as well as from increased competition by drought tolerant hardwood forest species.

Conclusions about the fate of existing young stands appear to be difficult. Although many of these sites could lose suitability regarding young life stages, which means that they might be no more suitable for the establishment and growth of new stands in the future, established stands may survive. Further maturation including growth of the root system is expected to make plants less prone to drier conditions (Rood *et al.* 2008) and sites may still provide conditions suitable for older vegetation.

Along most large rivers in Central Europe, riparian softwood forests currently suffer from a lack of sexual regeneration due to restricted morphodynamics, which are important for creating competition free, bare sites that allow the establishment of seedlings (Hughes *et al.* 2001). Indeed, we could not model seedling stages, since hardly any seedlings were detectable. Though climate change is expected to increase the frequency of more extreme flooding events (Dankers *et al.* 2008; Kundzewicz *et al.* 2010), which are important drivers for erosion and sedimentation processes to create bare ground sites (Geerling *et al.* 2008), it remains unclear to what extent such extreme events will occur and how they will shape respective processes (Kundzewicz *et al.* 2010). Even if intensive flooding events facilitated the germination and preliminary establishment of seedlings due to an extension of bare ground sites, it is likely that a future intensification of drought periods would override this positive effect since riparian willow and poplar seedlings are highly dependent on sufficient moisture for their establishment (Mahoney & Rood 1998). Consequently, if extended low discharges will occur as a result of climate change, the establishment of natural recruitment may become even further reduced compared to current conditions (Rood *et al.* 2008).

In contrast to seedlings, cuttings generally tolerate broader environmental conditions. This makes them less susceptible to changes in hydrology, but also to sedimentation and mechanical influences (Moggridge & Gurnell 2009). Hence, vegetative propagules could have a better chance of survival. Considering the expected changes in abiotic conditions and thereby the further increasing restrictions of natural sexual regeneration, the importance of reforestation projects at hydrologically suitable sites to enable long term persistence of riparian softwoods is additionally underlined.

Management options for restoring floodplain softwood forests under climate change

Young vegetation habitats should be chosen for reforestation activities (Mosner *et al.* 2011). However, as we could demonstrate there is large variability regarding the amount and location of suitable planting habitat if the whole range of possible conditions is considered. The large uncertainty due to the range of realisations, all being equally likely, as well as changes in site suitability in the course of the time is a particular problem for the selection of conservation sites (Carvalho *et al.* 2011; Erwin 2009). Therefore, a strategy to further increase the success of future plantings could be the selection of planting sites based on the entire ensemble of forecasts of different discharge realisations. This would allow the identification of sites predicted being suitable under the whole range of different realisations, a “no regret”-strategy (Araujo *et al.* 2007; Carvalho *et al.* 2011).

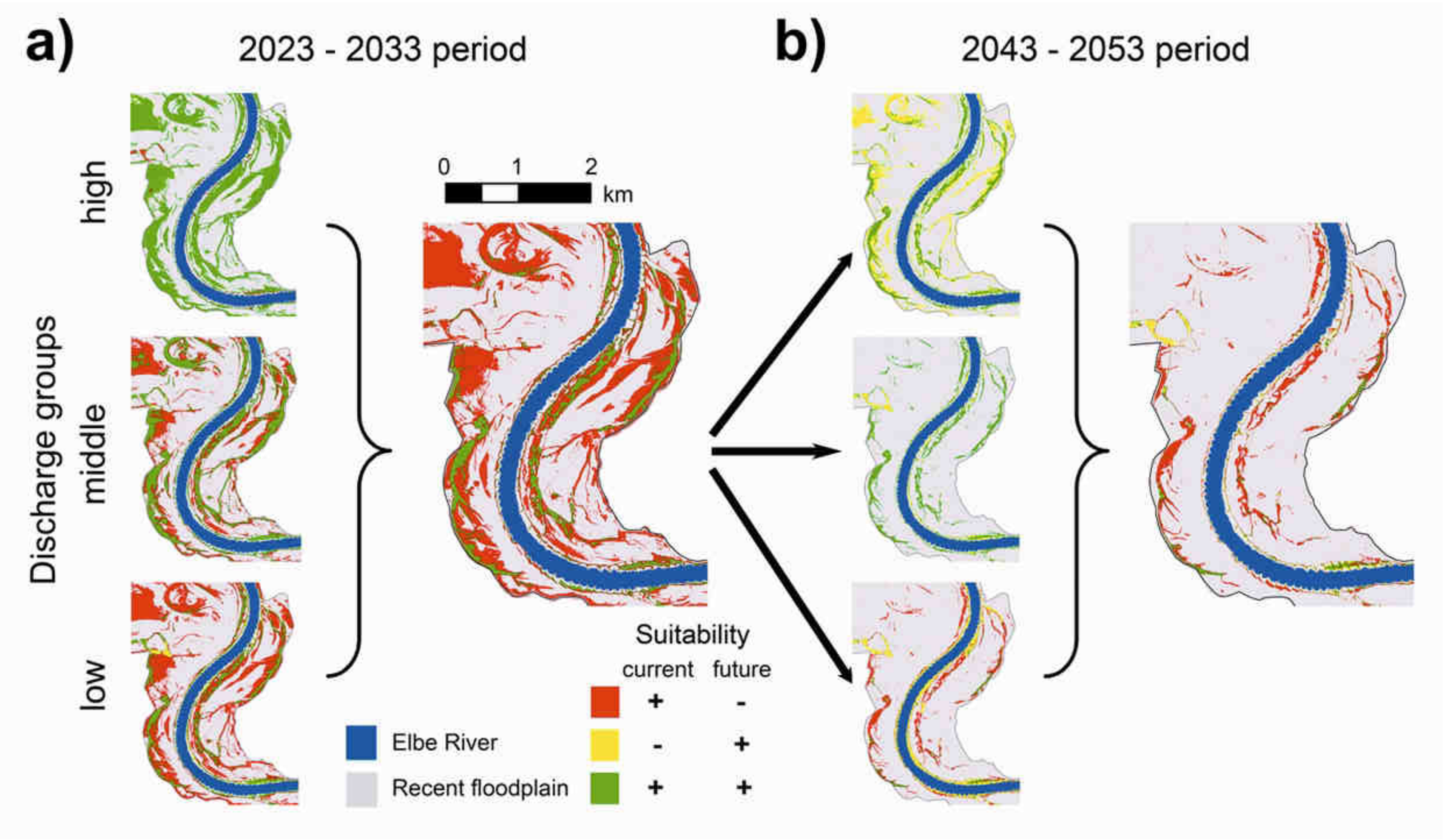

Figure 6: Projected habitat suitability for tree plantings under future conditions exemplified for a section of the study area. Displayed are: a) habitat suitability for the near future (2023-2033) with intersections of the five realisations for each of the three discharge groups (left) and the intersection of all discharge groups (right), b) habitat suitability for the far future (2043-2053) with intersections of the five realisations for each of the three discharge groups (left) and the intersection of all discharge groups (right). Note: Near-future suitability is identified by intersecting current and 2023-period conditions, whereas suitability of the 2043-period is evaluated based on the intersection of near-future and far-future conditions.

We could demonstrate that moderate decreases in discharge lead to a habitat shift towards lower elevations in the floodplain such as oxbow lakes and floodplain depressions. The role of such low elevation sites as refugia for woody pioneer species has recently been stated by Stella *et al.* (2011). As most of the floodplains of modified rivers are subject to floodplain aggradation over time (Buijse *et al.* 2002; Steiger *et al.* 2005) and morphodynamics are generally lacking, low elevation sites are of strongly limited availability. However, if discharge decreases will be as strong as the ones projected for the far future regarding the middle and low discharge scenario groups, even today's low elevation sites will turn into sites too dry for the growth of riparian softwood forest species. Floodplain lowering by excavation could hence be an effective restoration strategy (Geerling *et al.* 2008) buffering against the loss of suitable habitat for riparian softwood forest species under future conditions. At the same time, such excavations would provide bare ground sites facilitating sexual recruitment.

However, neither planting of riparian softwood forests nor floodplain excavation serves as a sustainable mitigation strategy, since both types of measures have to be repeated at regular intervals (Baptist *et al.* 2004; Geerling *et al.* 2008). An alternative could be process-oriented restoration such as reconnection of abandoned channels, increased overbank flooding etc. (Beechie *et al.* 2010). This would foster morphodynamics in the floodplain as one of the essential mechanisms behind successful, natural recruitment of riparian softwood forests leading to a self-sustainable system (Gonzalez *et al.* 2010b). Palmer *et al.* (2008) stated that increases in drought will leave fewer solutions to cope with climate change outcomes and species adapted to flooding could actually turn out to be the losers in such systems. However, as dynamics are an intrinsic feature of floodplain ecosystems to which species are adapted to and which can buffer anthropogenic impacts, renaturalisation of rivers and floodplains at least offers the chance for the system to readjust itself in the face of climate change thereby serving as a real adaptation strategy.

Acknowledgement

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Appendix

Table A.1: ANCOVA results of water level fluctuations (WLF) as the response variable against distance to the river (continuous predictor) and discharge group (categorial predictor).

Source	df	MS	*F*	*P*
Distance	1	5.5622	624.713	<0.001
Discharge group	5	0.0019	0.219	0.9544
Distance * discharge group	5	0.0041	0.466	0.8014
Residuals	249	0.0089		
Adj. R^2	0.704			

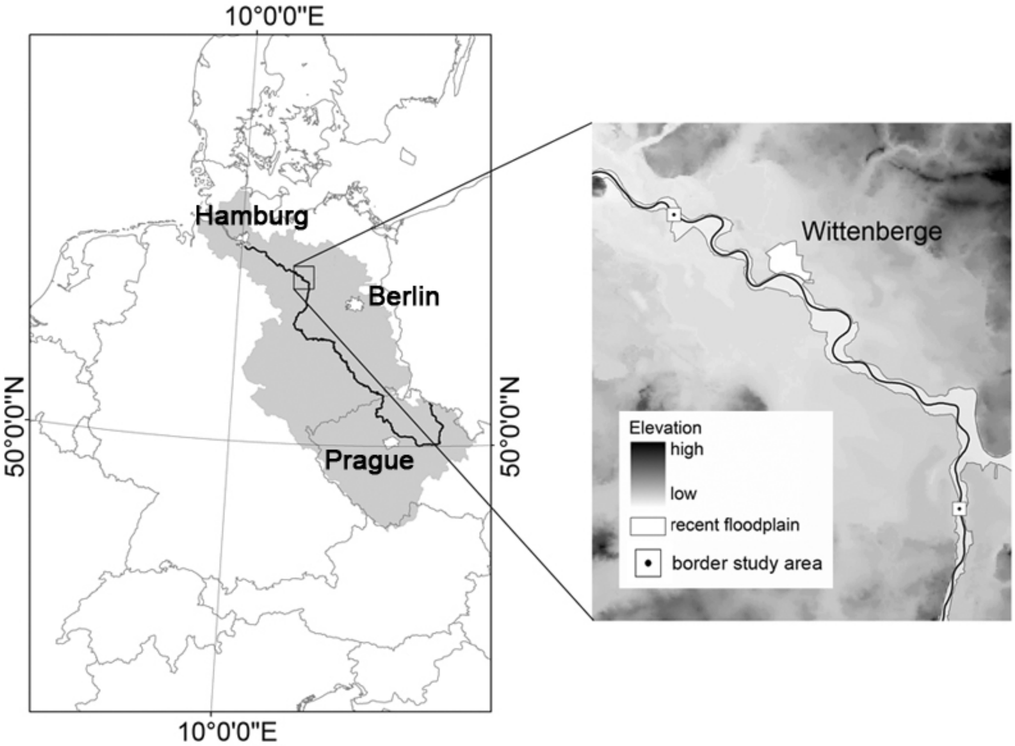

Figure A.1: Location of the Elbe River basin indicated in grey (left) and the detailed position of the study area in the vicinity of Wittenberge (right).

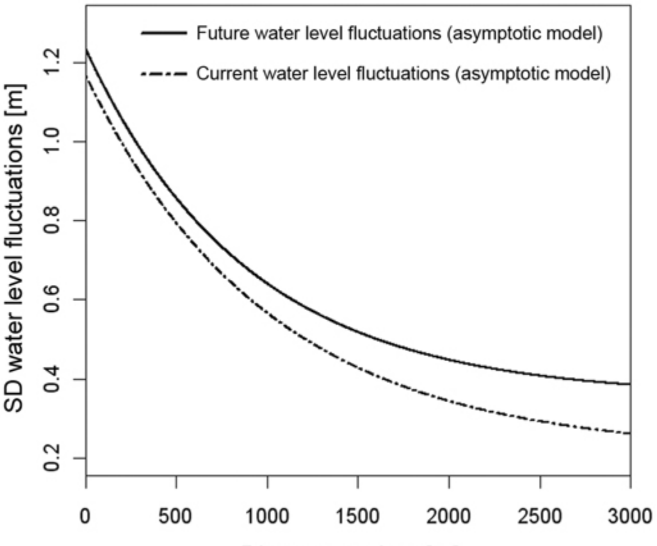

Figure A.2: Asymptotic models (based on ANCOVA results) of the relation of water level fluctuations (WLF) of current (dashed line) and future conditions (solid line) and distance to the river.

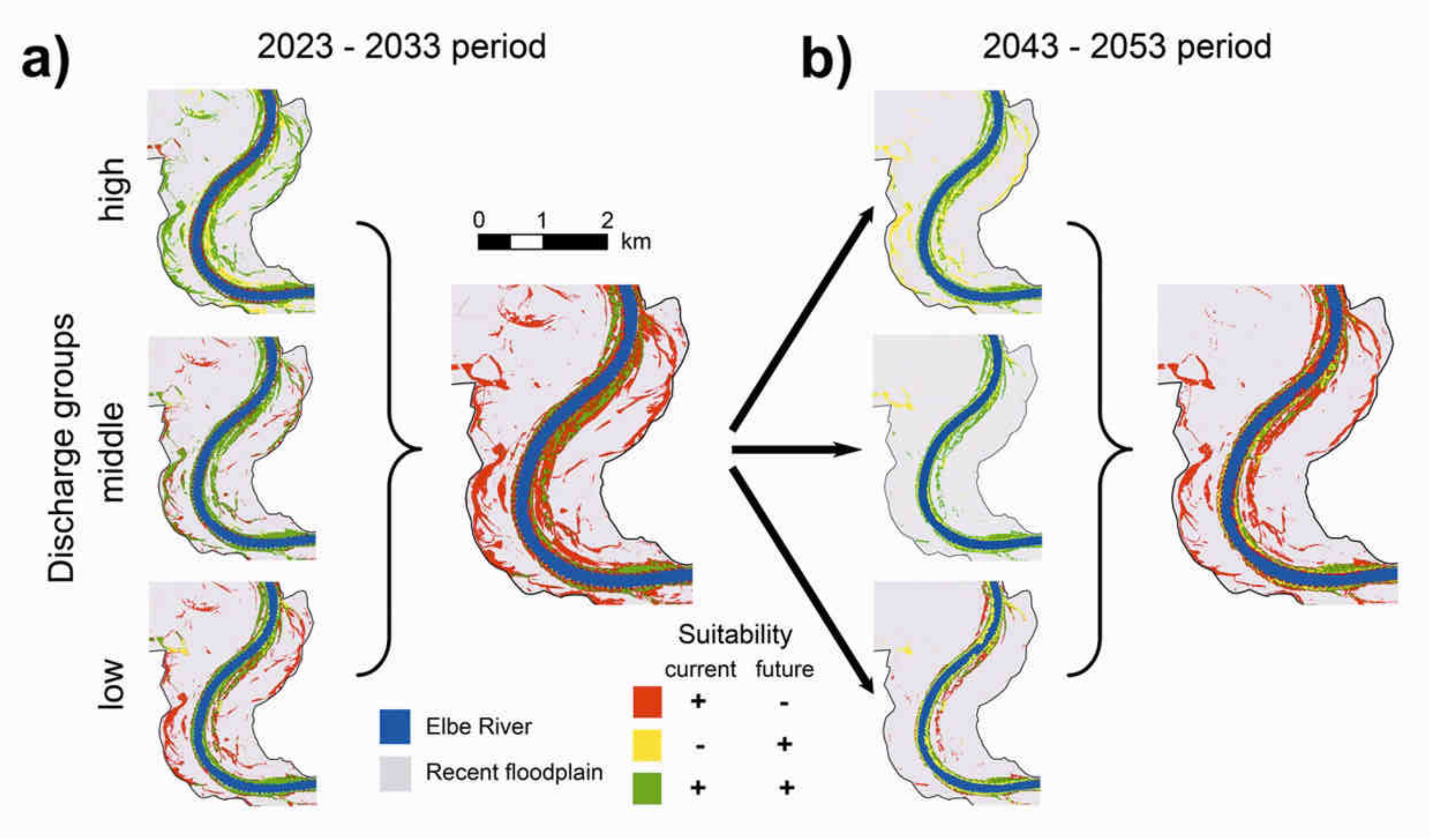

Figure A.3: Projected habitat suitability for shrub plantings under future conditions exemplified for a section of the study area. Displayed are: a) habitat suitability for the near future (2023-2033) with intersections of the five realisations for each of the three discharge groups (left) and the intersection of all discharge groups (right), b) habitat suitability for the far future (2043-2053) with intersections of the five realisations for each of the three discharge groups (left) and the intersection of all discharge groups (right).

Note: Near-future suitability is identified by intersecting current and 2023-period conditions, whereas suitability of the 2043-period is evaluated based on the intersection of near-future and far-future conditions.

Chapter 6

Floodplain willows in fragmented river landscapes: Understanding spatio-temporal genetic patterns as a basis for restoration plantings

Eva Mosner, Sascha Liepelt, Birgit Ziegenhagen & Ilona Leyer

Under review

Abstract

In Central Europe, floodplain fragmentation by dykes and river regulation by dams has led to a fundamental loss of riparian softwood forests and dramatically restricted natural regeneration of the Salicaceae species involved. As a consequence, reforestation is one of the widely-used measures to maintain this valuable vegetation type. Knowledge about the genetic population structure of existing stands of willows and poplars is necessary to preserve their genetic potential in the long term. In this study, we investigated clonal and genetic diversity patterns of *Salix viminalis* for 23 stands, taking into account young and old age classes and locations in front of and behind the dykes along the Elbe River, Germany. Codominant microsatellites were used in order to assess effects of stand and floodplain fragmentation and to evaluate the extent of clonal structures of a representative riparian softwood species. We detected considerable amounts of clones almost exclusively in old and young stands in front of the dykes with old stands exhibiting the largest number of clones. Clones mostly covered distances of less than 10 m, but single long-term dispersal events were also detected. Genetic diversity patterns revealed one continuous population with no distinction between the different stand types although a certain small-scale spatial genetic structure was identified. Our study suggests that riparian softwood forest species have efficient dispersal strategies to cope with altered floodplain conditions from a genetic point of view. On the basis of the results, management advice is given for selecting genetically suitable planting material for restoration purposes.

Introduction

Riparian softwood forests are a major vegetation type in floodplain ecosystems, providing important ecosystem services such as high biomass production, sediment stabilization, disturbance regulation, water purification and retention as well as accommodating high levels of biodiversity (Ward *et al.* 2002). Simultaneously, they are one of the most endangered habitat types in Europe, hence listed in Annex I of the European Habitats Directive (93/43/EEC). The main causes for the threat of riparian softwood forests are human impacts such as river regulation for navigation and hydroelectric power production as well as floodplain fragmentation by dykes (also called levees) for flood protection and land use intensification (Tockner & Stanford 2002). The latter in particular has led to a dramatic decrease in the actively inundated area along rivers all over the world (Gergel *et al.* 2002; Tockner & Stanford 2002, BMU & BfN 2009). Floodplain fragmentation provokes changes in hydrological and disturbance conditions (Leyer 2004; Van Looy *et al.* 2004), as well as water dispersal restrictions, leading to changes in plant species composition (Gergel *et al.* 2002; Leyer 2006; Nilsson *et al.* 2010). For sites behind dykes, profound effects on the plant population level can be expected as well (Nilsson *et al.* 2010); however, there is a complete lack of knowledge regarding this topic.

Missing morphodynamics due to river training are one of the main causes for the lack of recruitment by seeds of the typical riparian softwood forest species such as *Populus nigra*, *Salix alba*, and *S. viminalis* (Guilloy-Froget *et al.* 2002; Hughes *et al.* 2001). These species, which are highly susceptible to competition during establishment, need bare ground and a proper sequence of suitable hydrological conditions after germination to regenerate successfully (Hughes *et al.* 2001). In strongly altered floodplains, sexual recruitment is almost completely lacking and consequently, mostly over-aged populations can be observed (Tockner & Stanford 2002).

Besides sexual regeneration, riparian softwood forest species are able to propagate vegetatively. Though asexual propagules need suitable establishment conditions as well, they can tolerate a broader spectrum of growing conditions (Hughes *et al.* 2001; Moggridge & Gurnell 2009). In floodplain systems affected by diminished natural disturbance, an increase in the ratio of asexual to sexual regeneration can be expected (Karrenberg *et al.* 2002;

Watkinson & Powell 1993). Finally, the combination of restricted/missing sexual regeneration and widespread clonal propagation might lead to a depauperation of genetic diversity.

Restoration of natural river flow dynamics that would re-establish natural disturbances are considered to be the most effective strategy to conserve riparian softwood forests and their self-sustainability (Hughes *et al.* 2005; Smulders *et al.* 2008). However, such strategies are hardly applicable along many of the large rivers worldwide where economical interests preponderate (Hughes *et al.* 2005). Hence, site-specific restoration initiatives such as floodplain forest plantings are commonly applied (Hughes *et al.* 2005; Winfield & Hughes 2002). In this context, the preservation of genetic diversity is an important task in the conservation of long term potential for adaptation to changing environments (Booy *et al.* 2000; Pautasso 2009; Storme *et al.* 2004). In order to conserve genetic diversity, knowledge about its present spatial distribution is necessary to be able to collect suitable planting material from donor populations. In this context, the presence of clonal structures could exhibit a severe problem as a study by Storme *et al.* (2004) on ex-situ measures for *P. nigra* revealed. They detected that a substantial proportion of the gene bank consisted of replicated genotypes. The study of Budde *et al.* (2011) in particular, where one single clone of the invasive *S. x rubens* was found to cover long stretches of several Patagonian river systems, points to the enormous potential of the Salicaceae species for vegetative propagation. Interestingly, the age of stands also seems to play a role in population structuring. Barsoum *et al.* (2004) identified different proportions of clonal structures for different age cohorts of *P. nigra*. Therefore, knowledge of clonal patterns is a prerequisite for an effective sampling of planting material.

In this study, we attempt to unravel patterns of clonality and genetic diversity in the riparian shrub species *S. viminalis* as a model species for highly endangered riparian softwood forests using nuclear microsatellite markers. We expect genetic imprints caused by floodplain fragmentation through dykes as well as by the age of stands. Thus, we sampled young and old-aged stands occurring in habitats in front of the dykes as well as stands behind the dykes along a stretch of 60 km of the Elbe River, Germany. The results constitute the scientific basis for capturing genetic diversity for ex-situ and in-situ measures. Moreover, sound management advice is given for selecting genetically suitable planting material for restoration purposes.

Materials and methods

Study species

The study species, *S. viminalis* L. (Common Osier/Basket Willow) is a characteristic shrub of riparian softwood forests in Central European lowland rivers. It is a diploid, dioecious, insect-pollinated species producing a vast number of primarily wind and secondarily water dispersed seeds. Seeds retain their germination capacity for only a short period of about 2 – 4 weeks. Besides its ability to reproduce sexually, *S. viminalis* is also capable of regenerating vegetatively from branches that are usually torn off during floods and swept away by the current (Karrenberg *et al.* 2002). Along the Elbe River, the species occupies low elevation sites along the river banks as well as in the actively inundated floodplain, is able to tolerate long periods of inundation and can withstand strong mechanical forces for example by flooding or ice shearing due to its vigorous resprouting capacities (Radtke *et al.* 2011). In the study area, the species exhibits an unequal sex ratio with a strong bias towards the female. Like the other riparian softwood forest species along the Elbe River, *S. viminalis* occurs only erratically in small stands or as single shrubs in the active floodplain.

Study area

The study area (Fig. 1) comprises a 60 km stretch along the lowland parts of the Elbe River (river km 415 – 475), Germany, around the city of Wittenberge (52° 59’ 41’’ N, 11° 45’ 12’’ E). The Elbe River is one of the largest rivers in Central Europe with a length of 1 094 km and a catchment size of approximately 148 250 km^2. The first dykes were built in the 12th century and flood protection activities were intensified during the 18th century, resulting in a continuous dyke line in the early 1820s (Scholten 2005) dividing the floodplain into two compartments, the recent floodplain (RF, still flooded in times of high water) and the older floodplain (OF, not flooded anymore). However, the Elbe River exhibits fairly natural flow conditions with pronounced high flows during winter and spring and extended low flow periods in late summer. Flooding during the vegetation period does occur from time to time. The average discharge for this river stretch is about 700 m^3 * sec^{-1}. Today, the recent floodplain covers only about 10 % of its original size (BMU & BfN 2009). The dominating land use type is mowed or grazed meadows. Only about 2.5 % of the recent floodplain is covered by riparian softwood forests comprising two different vegetation types, the aboreal Salicetum albae Issler and the shrubby Salicetum triandro-viminalis Lohmeyer (Mosner 2011).

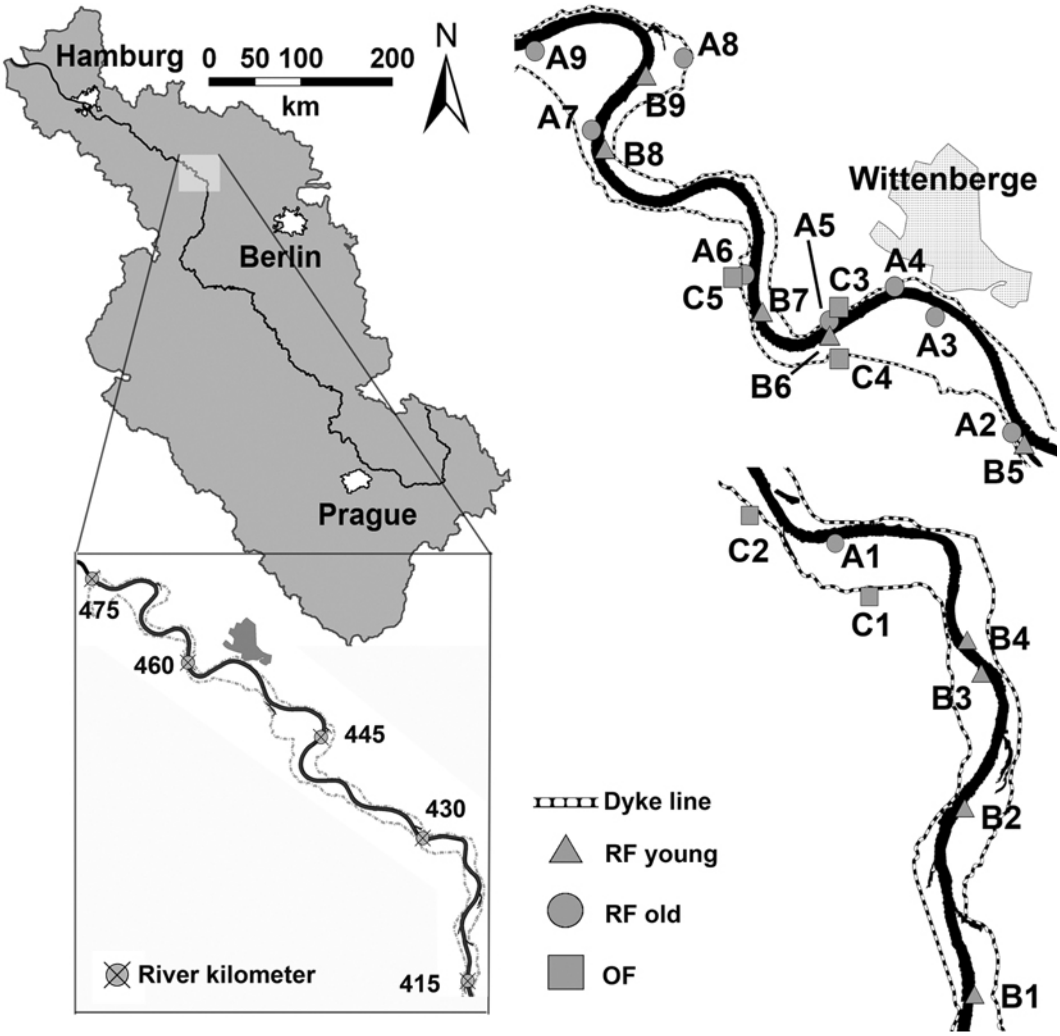

Figure 1: Map of the study area within the Elbe River catchment (upper left), the investigated river stretch (lower left) and the detailed location of the investigated stands (upper and lower right). RF = recent floodplain, OF = older floodplain.

Sampling and microsatellite analysis

In the years 2006 and 2007 we collected leaf material from 943 shrubs across 23 distinct stands of S. viminalis along the mentioned river stretch (Fig. 1 and Tab. 1). Only stands with ten or more ramets were sampled. We distinguished three different stand types based on floodplain compartment and age class: 1. old stands in the recent floodplain (RF old), 2. young stands in the recent floodplain (RF young), and 3. stands in the older floodplain (OF), which could not be categorised into “old” or “young” due to intermingled age structures in some stands. Age structure (old vs. young) was determined based on plant features such as diameter at ground level and height.

Ramets within each stand were randomly selected based on a grid design if more than 50 individuals were available. If less than 50 shrubs were present, leaf material from all plants was collected. The geographical position of each sampled shrub was recorded using a differential GPS (Leica Geosystems, Munich, Germany) with an accuracy of ≤ 1 m. The leaves were dried in paper bags, stored at room temperature and additionally dried at 36°C for 24 h prior to DNA extraction.

About 0.5 cm^2 of dried leaf tissue was first homogenised to a fine powder with a shaking mill (MM 200, Retsch, Haan, Germany) and genomic DNA was extracted following the protocol as described in Dumolin *et al.* (1995) with an additional final treatment of 0.5 µg RNase at 37°C for 30 min. Genotyping of the samples was conducted using six nuclear microsatellite markers (nSSRs): SB80, SB93, SB194 (Barker *et al.* 2003), SB349, SB904 (Hanley *et al.* 2002), and CHA591 (Hoshikawa *et al.* 2009). Two additional markers, SB38 and SB199 (Barker *et al.* 2003) were used to obtain additional genotypic information only for suspected clonal ramets.

Components for PCR reactions differed for the loci under study. Basically, two types of PCR cocktails (A and B) were used with A being used for loci SB80, SB 93, SB 194, SB 349, and SB 904 and B applied for loci SB38, SB 199, and CHA591. For each 25 µl (A) and 16.6 µl (B) PCR reaction, 30/20 (A/B) ng of template DNA, 5x/3.3x (A/B) PCR Green Buffer (Promega), primer specific $MgCl_2$-concentrations (Appendix 1, Table 1.1), 5 mM of each dNTP, 1 U/0.2 U (A/B) Taq polymerase (GoTaq, Promega), 0.2 mM of each primer (2mM; forward primer fluorescence labelled), and 0.2 µl BSA (20mg/ml; Fermentas & 10mg/ml Biolabs, A/B) were used.

The PCR cycles started with a denaturation step for 4 min at 94°C, followed by repeated cycles (Appendix 1, Table 1.1 for primer specific repeats) of denaturation (30 s at 94°C), annealing (45 s at primer specific annealing temperatures, Appendix 1, Table 1.1), elongation (30 s at 72°C), and ended with a final elongation (10 min at 72°C) including a final soak at 4°C. For SB38, a touchdown PCR was performed (Appendix 2 for details). PCRs were performed using Biometra T1 thermo cyclers (Biometra, Goettingen, Germany).

The amplification products were separated by capillary electrophoresis using a MegaBACE 1000 automated sequencer (GE Healthcare, Freiburg, Germany). Fragment sizes were determined with the internal size standard MegaBACE ET400-R (60 - 400 bp; GE Healthcare) and alleles were scored with Fragment Profiler 1.2 software (GE Healthcare).

Data analysis

Clonal structures

For the identification of clonal structures we used the “Multilocus Matches” option as implemented in GenAlEx 6.4 (Peakall & Smouse 2006). A first analysis was based on six loci applied to all samples. If the samples turned out to have identical six-locus-genotypes, two additional loci (SB38 and SB199) were applied to verify clonality. Moreover, 144 randomly selected samples of unique genets were also analyzed with SB 38 and SB 199 to gather data to calculate the probability of identity. Only ramets that yielded exactly the same genotypes were treated as clones.

To assess the discriminatory power of the multilocus-system to differentiate genotypes, the probability of identity for unrelated individuals (PI) and siblings (PI_{sibs}) was estimated using GenAlEx 6.4 for both the six-locus and the eight-locus marker system. To analyse the clonal patterns for the single stands more thoroughly, clonal diversity R was calculated with $R = (G-1)/(N-1)$, where G is the number of genets and N is the number of sampled plants within each stand (Arnaud-Haond *et al.* 2007). Clonal equitability, a measure for eveness of clone sizes regarding ramet numbers, was evaluated by calculating Pielou’s evenness (Arnaud-Haond *et al.* 2007). Both clonal richness and evenness were tested for differences between stand types by means of Kruskal-Wallis-Tests, since raw and transformed data did not fulfil the requirements for conducting parametric tests. When significant differences between stand types were identified, non-parametrical multiple test procedures according to the Behrens-Fischer type were conducted (Munzel & Hothorn 2001) as implemented in the “npmc”-package in R.

For comparison of frequency distributions of clone sizes between the different stand types, the Pareto distribution was used (Arnaud-Haond *et al.* 2007). The Pareto distribution is a power law distribution where the relationship between frequencies of ramets and clone sizes is described as $N_{\geq X} = a * X^{-\beta}$. While $N_{\geq X}$ is the total number of sampled ramets belonging to the clones comprising X (or more) ramets in the sample (Arnaud-Haond *et al.* 2007), α and β can be assessed fitting a regression of $\log(N_{\geq X})$ against log(X). If the fitted regression based on a log-log-scale leads to significant coefficients and a high R^2, conditions of a Pareto distribution are fulfilled. Accordingly, to compare the different stand types, an ANCOVA with log-transformed clone size (1-8) as the continuous (X), stand type as the categorical explanatory variable, and log-transformed frequency of ramets belonging to a specific clone size ($N_{\geq X}$) as the response variable was fitted.

Finally, vegetative dispersal distances of different stand types were assessed by comparing the frequency distribution of (Euclidean) distances between ramets of one clone for the different stand types applying a Kolmogorov-Smirnov-Test. All statistical tests were performed using R (R Development Core Team 2008).

Genetic structure of stands

The following analyses of genetic structure and genetic diversity were based on a reduced data set where only genets with one single individual were included. As clonal structures are likely to be the result of hydrochorous propagation, the ramet located most upstream was chosen for each clone. The sample size for population genetic analyses was 825 individuals.

First of all, we performed a Bayesian clustering analysis using STRUCTURE 2.3.2 (Pritchard *at al.* 2000) to reveal possible substructures within samples. 100.000 Monte Carlo Markov chain (MCMC) iterations after burn-in periods of 50.000 iterations with K ranging from 1 to 24 groups were run for 12 replicates under the assumption of an admixture model and correlated allele frequencies. Mean log-likelihood values at each value of K (ln Pr(X|K)) were calculated. Since L(K), the posterior probability of the data for a given K, does not always show a clear trend for the true K, the ad hoc quantity based on the second order rate of change of the likelihood function (ΔK) was used (Evanno *et al.* 2005) to identify the optimal number of clusters. To visualize potential substructures, a Principal Coordinates Analysis (PCoA) based on Nei's unbiased pairwise genetic distances for the single stands was performed as implemented in GenAlEx. Values for the first two coordinates were plotted.

Furthermore, we evaluated spatial genetic structure (SGS) by means of spatial autocorrelation analysis using the software SPAGeDi 1.2 (Hardy & Vekemans 2002). Average pairwise kinship coefficients (F_{ij}) as a multilocus average of genets were calculated according to the approach of Loiselle et al. (1995) for the predefined distance classes and the significance of the average kinship coefficient per distance class was tested by 10.000 permutations.

Genetic diversity of stands

To assess differences in genetic diversity between the different stand types, allelic richness R_t based on rarefaction (ElMousadik & Petit 1996) with a sample size of N=10 was calculated. Moreover, the inbreeding coefficient F_{IS} (Weir & Cockerham 1984) was computed and its significance was tested by a permutation procedure of 2760 randomizations. Both measures were calculated using FStat 1.2 (Goudet 1995). Finally, Nei's gene diversity was estimated using Arlequin 3.1 (Excoffier *et al.* 2005). To test for differences between stand types, a Kruskal-Wallis-Test with stand type as the explanatory variable was conducted for all three measures.

Results

Clonal structures

The probability of identity PI and P_{sibs} of the six marker system was 3.0 $*10^{-7}$ and 3.8 $* 10^{-3}$, respectively and PI and P_{sibs} of the eight marker system was $1.3*10^{-9}$ and 5.2 $* 10^{-4}$, respectively. Thus, the systems can be regarded to be sufficient to identify clonal structures. While 749 unique genotypes were identified, about one fifth of the total sample size (194 samples) were organised into 78 clones. Within the 23 stands, we detected substantial amounts of clones. Only six stands revealed no clones at all. Four of these stands were located in the older floodplain and only one each out of nine for both young and old stands in the recent floodplain held no clones (Tab. 1). Clonal diversity ranged from 0.611 to 1 (Tab. 1) and differed significantly between stands of the recent and older floodplain ($\chi^2_{2,21}$=10.022, p=0.006**; Fig. 2). Clonal evenness ranged between 0.716 and 1 (Tab. 1) and differed also between floodplain compartments (data not shown). Frequency distributions of clone sizes and dispersal distances of ramets were only assessed for the stands in the recent floodplain due to only one clone group in the older floodplain. Both stand types of the recent floodplain followed a Pareto distribution regarding the frequencies of clone sizes and no significant differences among stand types could be detected (clone size: $F_{1,9}$ 68.61***, stand type: $F_{1,9}$ 1.90 ns, clone size x stand type: $F_{1,9}$ 0.002 ns). Clone groups with just two ramets exhibited by far the highest frequency with a total of 52 pairs (33 RF old/ 19 RF young). Clone groups with three ramets occurred in 11 cases (9 RF old/ 2 RF young) and eight groups with four ramets (6 RF old/ 2 RF young). The largest clone group with eight ramets occurred in one of the young stands.

Regarding dispersal distances of vegetative propagules, the Kolmogorov-Smirnov test revealed significant differences between ramets of clones of the two recent floodplain stand types (D = 0.5253, p = 0.000***). While patterns for distances above 10 m showed similar frequencies for the old and young stands, old stands comprised far more ramets within the first distance interval of up to 10 m (Fig. 3). In three cases, long distance vegetative dispersal was detected with a maximum of 1.9 river kilometres. In all cases, young individuals were found downstream of the old ramets.

Table 1: Statistics of gene diversity and clonal diversity for the 23 analysed stands of *S. viminalis* based on six (gene diversity) and eight (clonal diversity) microsatellites.

Nr.	Location	Stand Type	River km	N	G	R_t	H_O	H	F_{IS}	HWE	Clonal diversity	Pileous Evenness
A1	Werben	RF old	429	28	18	5.09	0.657	0.690	0.049	ns	0.630	0.741
A2	Losenrade	RF old	451	46	34	5.94	0.727	0.747	0.027	ns	0.733	0.802
A3	Wittenberge railroad	RF old	455	50	43	6.16	0.713	0.740	0.037	ns	0.857	0.894
A4	Wittenberge port	RF old	456	50	36	6.02	0.770	0.766	-0.005	ns	0.714	0.786
A5	Wittenberge scrub	RF old	457	51	44	5.69	0.680	0.722	0.059	ns	0.860	0.896
A6	Wahrenberg	RF old	461	50	42	6.08	0.722	0.744	0.03	ns	0.837	0.879
A7	Hohe Garbe East	RF old	467	22	15	5.04	0.640	0.701	0.09	ns	0.667	0.778
A8	Cumlosen	RF old	469	37	23	6.16	0.752	0.769	0.022	ns	0.611	0.716
A9	Hohe Garbe West	RF old	473	51	51	5.72	0.716	0.693	-0.034	ns	1.000	1.000
B1	Sandau	RF young	416	38	29	6.06	0.741	0.749	0.011	ns	0.757	0.824
B2	Havelberg	RF young	421	33	27	6.25	0.685	0.747	0.085	ns	0.813	0.868
B3	Räbel	RF young	424	50	49	4.99	0.690	0.678	-0.017	ns	0.980	0.985
B4	Havelberg sluice	RF young	425	14	10	5.50	0.750	0.766	0.022	ns	0.692	0.819
B5	Losenrade	RF young	451	35	28	5.90	0.768	0.731	-0.052	ns	0.824	0.854
B6	Wahrenberg	RF young	458	47	45	6.36	0.740	0.756	0.023	ns	0.957	0.968
B7	Wittenberge North	RF young	460	48	42	6.10	0.702	0.713	0.016	ns	0.894	0.906
B8	Cumlosen South	RF young	467	42	39	4.03	0.717	0.619	-0.162	* Ex	0.927	0.947
B9	Cumlosen Middle	RF young	469	12	12	6.10	0.583	0.692	0.163	ns	1.000	1.000
C1	Werben East	OF	429	50	49	5.62	0.734	0.755	0.029	ns	0.980	0.985
C2	Werben West	OF	431	41	41	4.99	0.743	0.702	-0.059	ns	1.000	1.000
C3	Wittenberge scrub	OF	457	50	50	5.76	0.650	0.685	0.051	ns	1.000	1.000
C4	Wahrenberg-Wittenberge	OF	458	50	50	6.23	0.672	0.743	0.098	* Def	1.000	1.000
C5	Wahrenberg	OF	461	48	48	5.60	0.763	0.730	-0.045	ns	1.000	1.000

Stand Type: RF – recent floodplain, OF – older floodplain; N = number of samples, G = number of genotypes, R_t = allelic richness after rarefaction; H_O = observed heterozygosity, H = gene diversity, F_{IS} = inbreeding coefficient, HWE = test for significant deviation from Hardy-Weinberg-Equilibrium (ns: not significant, * significant at $p = 0.05$, Ex = heterozygosity excess, Def = heterozygosity deficiency).

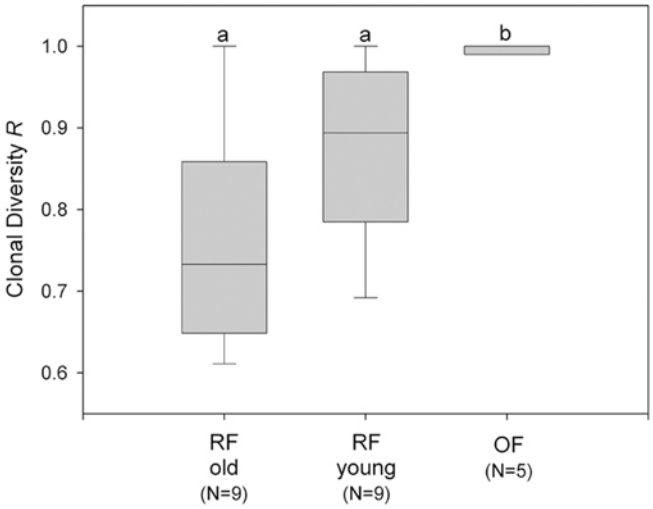

Figure 2: Box whisker plots of clonal diversity for the three investigated stand types. RF = recent floodplain, OF = older floodplain. Different letters indicate significant differences according to the multiple comparison procedure at p = 0.05.

Genetic structure of stands

The Bayesian cluster analysis revealed no clear pattern for the grouping of stands, neither for the mean log likelihood, nor for the ΔK approach (data not shown). Results of the PCoA were congruent with this. The first two axes explained almost 50 % of variation (axis 1: 26.2 %, axis 2: 23.2 %), but no clear pattern could be identified, neither regarding geographical position along the river course, nor regarding age class or floodplain compartment (Appendix 3, Fig. 3.1).

Analysis of spatial genetic structure showed significant spatial autocorrelation within 700 m. However, mean kinship coefficient already dropped to less than a half within the first 30 to 40 m, thereafter decreasing gradually to very low values (Fig. 4).

Genetic diversity of stands

Allelic richness after rarefaction was similar among the different stands and ranged between 4.03 and 6.36 (Tab. 1). Inbreeding coefficient F_{IS} varied between -0.16 and 0.16 (mean: 0.02) but only two stands showed significant deviations from Hardy-Weinberg-Equilibrium with an excess of heterozygotes in one of the young stands and a heterozygote deficiency for one of the stands in the older floodplain (Tab. 1). All stands showed high levels of gene diversity ranging between 0.62 and 0.77 (Tab. 1). Kruskal-Wallis-Tests for all diversity measures showed no significant differences between the three stand types.

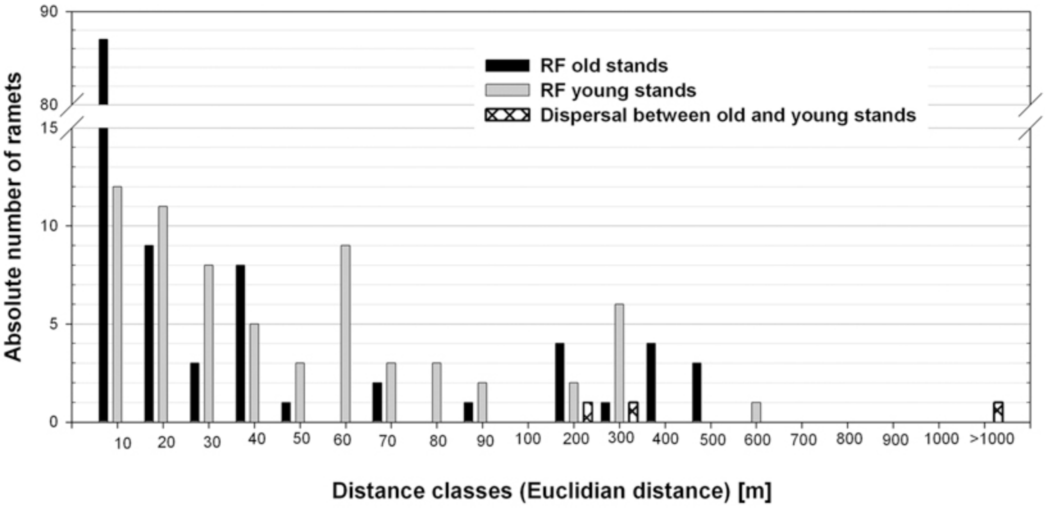

Figure 3: Frequency distribution of distances between ramets of the same clone for different stand types. RF = recent floodplain, OF = older floodplain. The third category displays clones for which ramets in both old and young stands in the recent floodplain were detected.

Discussion

Spatio-temporal patterns of clones

We found an interesting pattern of clones in relation to the age and location of the analyzed stands. Almost no clones occurred in the older floodplain, which is at first glance in contrast to the expectation that decreased disturbance intensities should increase the ratio of asexual to sexual regeneration (Watkinson & Powell 1993, Karrenberg 2002). The reason behind this is that decreased disturbance leads to a lack of bare ground for the germination of seeds. Indeed, in the older floodplain, bare-ground sites are almost absent, although sexual regeneration can occur along the edges of ponds. Here, inundation periods are long enough to disable the growth of competitive species and afterwards sufficient soil moisture for seedling establishment is available. Vegetative regeneration in the older floodplain is even less likely to occur than sexual regeneration. Mechanical forces due to water flow are the prerequisite for clonal propagation (Barsoum *et al.* 2004), the former completely absent behind the dykes. Thus, regeneration relies mainly on seedlings which is the reason why in the older floodplain, the ratio of asexual to sexual regeneration is very low.

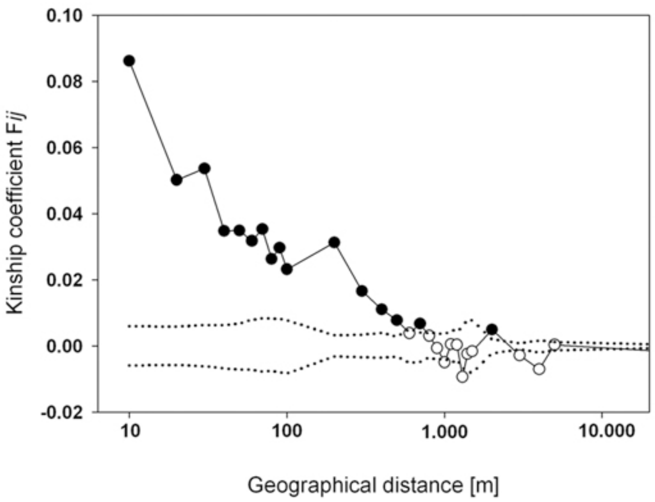

Figure 4: Spatial autocorrelogram of pairwise kinship coefficients of genets of *S. viminalis.* Mean kinship coefficients are given (filled symbols – significant deviation, empty symbols – non-significant deviation). The dashed line delimits the 95 % confidence interval of the kinship coefficient for random pairs of genets based on a permutation procedure (n=10 000). Note the log-scale of the x-axis.

In contrast, in the recent floodplain, strong mechanical forces lead to bending of shrubs followed by vigorous resprouting (Radtke *et al.* 2011). This causes small-scale clonal patterns, as found for the old as well as the young stands in the recent floodplain. However, old stands exhibited a larger amount of such clones, nearly seven times as high compared to the young stands. It can be assumed that the more frequent exposure of old stands to flooding over time causes this pattern (Barsoum *et al.* 2004).

Fairly weak clonal structures within the young stands suggest that instead of exploiting colonized sites, clonality acts as a further dispersal strategy besides sexual regeneration to reach and populate new sites. In systems of large disturbance intensities in particular, where high turnover rates of suitable sites can be expected, vegetative regeneration is a useful strategy (Karrenberg *et al.* 2002, Silvertown 2008). Long-distance dispersal of more than 1 km found in our and also in studies on *P. nigra* supports this aspect (Barsoum *et al.* 2004; Rathmacher *et al.* 2010) and the ability of many riparian softwood forests species to shed living branches suggests an adaptation to promote this form of dispersal (Beismann *et al*. 2000, Rood *et al.* 2003). Moreover, sexual regeneration is restricted to spring when the seeds are released. Since specific establishment conditions during these phases are necessary, sexual regeneration can be a rare event even in floodplains exhibiting natural, unregulated flow and disturbance conditions (Hughes 2001). In contrast, vegetative dispersal can occur throughout the whole year and propagules are able to establish under a larger variety of environmental conditions compared to seedlings (Moggridge & Gurnell 2009). In this way, vegetative propagules can act as a backup strategy for years without the successful establishment of seedlings. Besides, vegetative propagules might function as “engineers” to facilitate the establishment of seedlings due to soil stabilization and by providing shelter (Gurnell & Petts 2006, Moggridge & Gurnell 2009).

Genetic population structure of stands and patterns of genetic diversity

Generally, fragmentation can be considered to have fundamental effects on genetic diversity if the gene flow in the landscape is restricted by limited pollen and/or seed dispersal (Aguilar *et al.* 2008). In spite of the highly fragmented softwood forest woodlands, no clear population structure in the study area could be detected, neither spatially nor among age cohorts. In combination with evenly distributed high levels of genetic diversity, this suggests that the gene flow acts efficiently across fairly large distances and also across floodplain compartments. A continuous population structure can be assumed, at least across the investigated scale. Smulders *et al.* (2008) even found that genetic patterns of *P. nigra* populations within and across catchments largely overlapped concluding that differentiation takes place on even larger scales than just single rivers. In other riparian plant species, evenly distributed genetic diversity throughout different age cohorts as well as throughout populations was explained by hydrochory as an important dispersal mechanism (Jacquemyn *et al.* 2006; van Looy *et al.* 2009). Since hydrochory can clearly be excluded as a dispersal mode for softwood forest stands behind the dykes, anemochory is the dominating dispersal mode enabling colonization at these sites. Obviously, putative barriers, such as dykes as well as large distances between stands do not restrict gene flow for such species. Consequently, threats from fragmentation are probably far less severe than often expected (Kramer et al. 2008). However, it has to be taken into consideration that woody species exhibit long generation times and consequences of fragmentation may require several generations to become apparent in the genetic structure of the populations (Kramer *et al.* 2008; Pautasso 2009). Therefore, the impact of fragmentation processes on softwood forest species may come into effect only after centuries.

Even though the willow stands are connected through gene flow, small-scale genetic structure was observable. Spatial genetic structure, i.e. stronger relatedness of neighboured individuals compared to more distant ones, is often interpreted as a restriction in dispersal ability (Vekemans & Hardy 2004). For *P. nigra,* such structures have been found as well and were interpreted that way (Imbert & Lefevre 2003; Rathmacher *et al.* 2010). This is not in contradiction with the previously postulated highly efficient gene flow in *S. viminalis* as this is insect-pollinated, which could explain the positive spatial autocorrelation below 200 m due to the rather short distances of pollen flow (Steffan-Dewenter & Tscharntke 1999). Also, we cannot exclude a deposition of seed clouds which represent a cohort of maternal half-siblings (Born *et al.* 2008; Slavov *et al.* 2010). Since the establishment of the seeds is dependent on the availability of conditions, which do not occur everywhere and every year, small scale patches of related individuals may be the consequence (Rathmacher *et al.* 2010). Obviously this has no effect on the overall connectivity.

Conservation aspects for the selection of suitable restoration material

The findings of our study infer guidelines for the selection of planting material from riparian softwood forest species of fragmented river landscapes for either in situ or ex situ conservation measures to avoid sampling of closely related individuals.

1. As clonal structures occur rather abundantly across short distances (Fig. 3), individuals from which branches are collected should exhibit distances of more than ten metres.
2. The likelihood of sampling clonal structures is higher for old stands compared to young stands occurring in the recent floodplain. Clonal structures can practically be excluded for stands in the old floodplain if not planted. From that point of view, stands in the older floodplain and young stands in the recent floodplain should be preferred when collecting planting material. However, as sites in the older floodplain exhibit different hydrological conditions regarding flood duration and water level fluctuations compared to the recent floodplain, possible adaptations of stands to these conditions should be considered which are not reflected by neutral markers such as microsatellites. Therefore, planting sites for such material should resemble respective conditions.
3. Since no temporal or spatial pattern of genetic diversity was detectable, stands along river stretches can be regarded as being one single population with genetic diversity dispersing across the whole area. Thus, not all stands have to be sampled to cover existing diversity. However, since stands display genetic similarity across distances of about 1 km, several stands comprising larger distances between each other should be selected.

Conclusion

Taken as a whole, our results of genetic population patterns point to the highly effective strategy of *S. viminalis* of dealing with the great uncertainty of environmental conditions present in floodplain ecosystems. The combined sexual and vegetative reproduction enables the species to colonize newly established and often distantly located sites. This maintains high levels of genetic diversity and overcomes floodplain fragmentation and the reduction in floodplain dynamics from a population genetics point of view. No detrimental effects on genetic structure are evident on a regional spatial scale at this point in time. Kramer et al. (2008) stated that genetic pressures due to fragmented populations might not be as immediate a concern as ecological aspects. Indeed, the most important threat to the persistence of riparian softwood forest species is the severely restricted morphodynamics necessary for natural regeneration by either seeds or vegetative propagules. Long-term persistence of riparian softwood forests can only be assured if conservation and restoration measures address this urgent ecological problem (Leyer *et al.*, in press). As well as this, vital and genetically diverse populations need to be maintained and established to conserve the genetic potential for sexual regeneration in the long term.

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Appendix

Appendix 1

Table 1.1: Primer specific $MgCl_2$ amounts, annealing temperatures and number of cycles used in PCR.

Primer	$MgCl_2$ (mM)	Annealing temperature (°C)	Number of cycles
SB 38	1.8	see Appendix 2	see Appendix 2
SB 80	2.5	56	30
SB 93	2.5	56	30
SB 194	2.5	51	30
SB 199	2	52	27
SB 349	1.75	54	30
SB 904	1.5	54	33
CHA 591	2	53	25

Appendix 2

Protocol of touchdown PCR for SB38

1. 5 min at 95°C

<u>for 2. - 4.: 11 cycles with temperature decrease of 1°C per cycle</u>

2. 40 sec at 95°C
3. 45 sec at 60-49°C
4. 40 sec at 72°C

<u>for 5. – 7.: 30 cycles</u>

5. 45 sec at 95°C
6. 45 sec at 53°C
7. 45 sec at 72°C
8. 10 min at 72°C
9. final hold at 4°C

Appendix 3

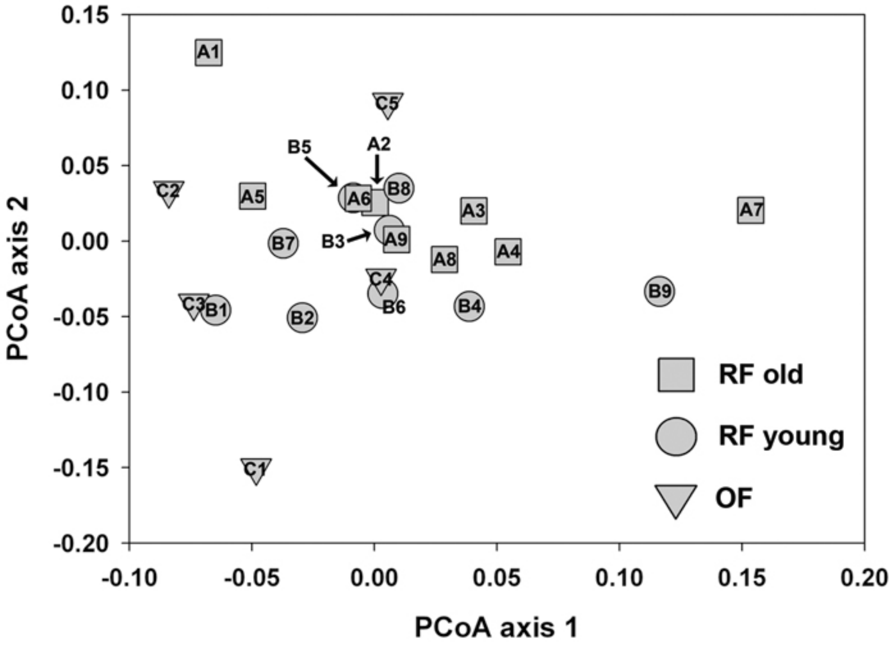

Figure 3.1: Principal coordinates analysis (PCoA) plot of the first two axes based on Nei's Genetic Distance *D* among stands. Numbers refer to stands described in Table 1. RF = recent floodplain, OF = older floodplain.

Chapter 7 – Discussion, Conclusion and Perspectives

The restoration of floodplain ecosystems in general and of riparian softwood forests in particular is a challenging task given the ecological requirements of species and communities on the one hand and the economical and societal demands of humans on the other. Though the often claimed process oriented restoration of river flow and morphodynamics will presumably not be accomplishable for most of the large rivers in Central Europe there is still scope for riparian softwood restoration in the form of restoration plantings as this thesis reveals. However, even plantings are subject to restrictions regarding flooding safety and above all, species' ecology has to be considered if restoration efforts are to be successful. In this context, the different aspects presented in this thesis deliver a basis to improve the success of restoration measures of riparian softwood forests.

Application of habitat distribution models in practice

The overall important role of hydrological conditions in structuring floodplain communities has long been recognized (Naiman & Decamps 1997; Blom 1999; Nilsson & Svedmark 2002; Ward *et al.* 2002). However, while basic habitat requirements for the successful (natural) establishment of riparian softwood species are well known (e.g. Hughes *et al.* 2001; Karrenberg *et al.* 2002; Barsoum 2002; Francis *et al.* 2005; Francis & Gurnell 2006), application of this knowledge in practice appears to be difficult as the failure of many such projects reveals (Stanturf *et al.* 2001; Andrews *et al.* 2010). The habitat models I developed were able to sufficiently describe the distribution patterns of the two riparian softwood vegetation types and their age classes on the basis of hydrological variables. In that way, modelling approaches as the one presented can serve in two different ways: Firstly, they can assist in identifying important variables influencing species distribution as well as often unapparent interactions of factors (Dormann 2007; Elith & Graham 2009). Thereby, a deeper understanding can be gained on how species' ecology shapes distribution patterns (Guisan & Thuiller 2005). On the other hand, models allow transferring ecological patterns into spatial information, i.e. identification of locations of suitable habitat. This information can then be used to assist the selection of suitable restoration sites considering species demands (Guisan & Thuiller 2005; Rodriguez *et al.* 2007), as it was done in paper I, III and IV. In that way, habitat distribution models can act as valuable contributions in planning reforestation measures.

Since the modelling approach was confined to a rather local scale transferability of modelling results in space and time should be tested to evaluate the generalisability of identified species-environment relationships (Pearman et al. 2008). Moreover, validation of models, i.e. employing models on a data set for the target region of application, should be conducted before models are used for projections e.g. to designate conservation areas (Bonn & Schroder 2001; Pearce *et al.* 2001; Vaughan & Ormerod 2005; Araujo & Guisan 2006; Randin *et al.* 2006). However, since floodplains are highly dynamic systems and relations of abiotic conditions can strongly vary across space and time, the transferability of specific models might be limited (Peters et al. 2008). Especially application of models across different river systems can be expected to have limitations given the different discharge regimes of rivers (e.g. Elbe River with peaks in late winter/early spring vs. Rhine River with highest discharges in summer due to snow melting in the Alps). Nevertheless, including a broad data basis, i.e. data from different river stretches or rivers with similar discharge regimes, collection of data from different time periods exhibiting distinct conditions, etc., might enable to identify the general underlying ecological patterns. In that way, generalisability of assumptions across scales could be tested.

Biotic aspects for softwood forest restoration

An important prerequisite for successful reforestation measures in highly variable environments such as river floodplains is to consider habitat suitability in relation to species life history. Regarding the investigated riparian softwood vegetation types partly distinct niches were occupied by the different age classes (paper I), which has significant implications for the selection of reforestation sites. Several authors have stressed the importance of including the life histories of species to disentangle autecological dynamics of species in river floodplain systems (Mahoney & Rood 1998; Nakamura *et al.* 2007; Merritt *et al.* 2010). Especially the role of the regeneration niche (sensu Grubb 1977), i.e. the conditions that plants experience during their establishment phase are crucial in ecosystems of high disturbance intensities like floodplains. Restoration activities that address specific species should take into account demands of ontogenetic stages. If not considered, restoration efforts might fail. Though, I did not test the models in the way that I experimentally surveyed establishment success of cuttings based on the model predictions for suitable and unsuitable planting sites. In this regard, some uncertainties remain on how sites, predicted to being appropriate habitat for young life stages, actually are suitable for cuttings (of only a few decimetres length and no “prolific” root system). However, modelling of newly established saplings was not possible since nearly no such life stages were detectable in the field. Moreover, the fate of seedlings and saplings during the first years of establishment are highly dependent on a proper sequence of suitable hydrological conditions (and related aspects such as sedimentation, soil moisture availability, etc.) as suggested by the recruitment box model introduced by Mahoney & Rood (1998). Thus, presence of saplings is not necessarily a good indication that conditions are principally appropriate for their long term establishment. As such, using sites suitable for (successfully established) young vegetation appears to be the best approach available. That plantings on such sites still could fail in the case of “abnormal” exceedingly moist or dry years is an inherent feature of highly dynamic floodplains and has to be accepted as one possible trajectory (Hughes *et al.* 2005). However, selection of reforestation sites based on the presented approach can be expected to increase the success of measures.

While abiotic conditions characterize the fundamental (Grinnellian) niche of species, species interactions in general lead to further restriction of suitable habitat, resulting in the realized (Eltonian) niche (Hirzel & Le Lay 2008). As the experimental study (paper II) revealed competition during early establishment phases plays not only an important role for seedling stages (Cooper *et al.* 1999; Hughes *et al.* 2001; Karrenberg *et al.* 2002), but also for vegetative propagules. Hence, not only abiotic factors and their interactions but also biotic influences should be a major concern regarding restoration activities. Generally, vegetative propagules have been reported to being less susceptible to environmental variations compared to seedlings (Moggridge & Gurnell 2009). Indeed, growth was not completely suppressed in our experiment, but performance under competition conditions was worse than without the competing species present. However, competition under experimental conditions was probably rather weak due to the set up of the experiment (e.g. maintenance of height of *Poa trivialis* at < 20 cm). Under natural conditions, competition by abundant grass species such as the reed canary grass, *Phalaris arundinacea*, can be expected to imposing much stronger competition levels for the establishment of vegetative propagules (Romano 2010). Thus, restoration measures by plantings will presumably be more successful if competition with other species, especially grasses, will be inhibited by measures such as regular mowing or mulching. In addition, many studies investigating the role of competition along stress/productivity gradients have revealed that competition effects change along such gradients, like inundation duration (Lenssen *et al.* 2003; Brose & Tielborger 2005; Toogood & Joyce 2009; Jung *et al.* 2009; Kotowski *et al.* 2010). A trade-off between life history strategies, i.e. competitive ability vs. stress tolerating ability, is the cause (Grime 1979). Thus, competition effects on riparian softwood species may act more severe under drier conditions compared to the other, physiologically bounding end (Sweeney *et al.* 2004; Kotowski *et al.* 2010). As such, counteracting competition might be more important for sites where hydrological conditions are suboptimal. As results on possible climate change effects suggest changes in hydrological conditions, interactions of different species occurring along inundation/water levels could become more important in the future (Ström et al. 2011). Hence the functioning of biotic interactions along abiotic gradients should be investigated to clarify under which conditions which factors are mainly structuring the observed distribution patterns.

Future prospects for riparian softwood forests

A central aspect of restoration measures should be their sustainability (Palmer *et al.* 2005). Generally, it can be stated that “active” restoration measures such as plantings (Jensen *et al.* 2006) have their shortcomings regarding this aspect. This is even truer when considering the potential effects of climate driven hydrological changes as paper IV revealed. Results indicate a loss of suitable habitat for extant vegetation, and even more for sites currently suitable for reforestation. Certainly, limitations of static modelling approaches to project future conditions exist, which are related to aspects such as: the role of correlative vs. causal relations of distribution patterns and environmental variables, spatial and temporal scales of studies, possible changes in species-environment relationships in the future, changes in biotic interactions, “new” combinations of environmental conditions, species plasticity and adaptation ability (Araujo *et al.* 2005; Heikkinen *et al.* 2006; Pearson *et al.* 2006; Dormann 2007; Araujo & Luoto 2007; Foody 2008; Beaumont *et al.* 2008; Trivedi *et al.* 2008; Randin *et al.* 2009). Though Central European riparian softwood forest species occur across a wide range of climate zones, climate change in Central Europe could lead to climatic conditions exhibiting characteristics of range edges of species. If so, macro-climatic variables could become important as well as the interactions of macro-climatic and small-scale hydrological conditions (e.g. under warmer and drier conditions the role of hydrological conditions could be more pronounced, Gonzalez *et al.* 2010b). As a consequence, species threats could be even more severe. On the other hand, even if investigations from the range edges would suggest strong plasticity of species and no such threats, regional adaptations and the occurrence of "ecotypes" still have to be considered which can result in ecological and genetic distinctness of populations of the same species (May *et al.* 2011). Hence, a combination of different scales should be employed to overcome problems of single scale approaches (Randin *et al.* 2009).

Another approach could be the usage of mechanistic models (also in combination with habitat models, Keith *et al.* 2008; Kearney & Porter 2009). In contrast to statistical approaches, such kind of models are based on causal mechanisms of species distribution patterns by modelling actual population dynamic processes such as establishment and mortality in relation to abiotic conditions (Kramer *et al.* 2008). This approach might also improve assessing climate change effects as future conditions are expected to be different from today's conditions. Increased frequencies of prolonged dry periods as well as of extreme flooding periods both occurring during the vegetation period are expected (Christensen & Christensen 2003; Kundzewicz *et al.* 2010). While no indication exists that a combination of single extreme events has detrimental effects on typical floodplain vegetation types (Ilg *et al.* 2008; Kramer *et al.* 2008), repeated occurrences of such events in tandem could exceed the resilience of characteristic floodplain vegetation types finally leading to an alternative community state (White & Stromberg 2011). Long-term experiments could enhance our knowledge regarding community dynamics in this context. However, many years of study might be necessary before useful results could be obtained (Ström *et al.* 2011).

In view of the ongoing and rapid climate change, genetic diversity of populations as a prerequisite for the adaptation ability of species to environmental changes becomes important (Booy *et al.* 2000; Pautasso 2009). Moreover, in order to conserve species, besides ecological aspects, knowledge about the genetic patterns of natural populations as a baseline for restoration measures is needed (Godefroid *et al.* 2011). As results of the genetic survey indicate (paper V), constitution of the existing softwood woodlands, though heavily under pressure in terms of ecological conditions, appear to be fine from a genetic point of view. Two aspects should be considered however:

First, all investigated stands along the Elbe River have been subject to modified river flow dynamics with respective consequences for population dynamics. Evaluating genetic diversity conditions are limited if no populations of natural, unconstrained rivers are available for comparison as a “real” reference state (Hughes *et al.* 2005). However, such reference systems are rare since nearly all European river systems are anthropogenically altered (Petts 1989; Tockner *et al.* 2009). Comparing patterns and measures of diversity identified in paper V with other studies of riparian softwood forest species reveal similar levels and authors state that losses of genetic diversity have not occurred yet (Imbert & Lefevre 2003; Pospiskova & Salkova 2006; Smulders *et al.* 2008; Rathmacher *et al.* 2010). This could either mean that periods of changes have not yet been long enough to have an impact on genetic levels (Van Looy *et al.* 2009) or else that such consequences are actually little threatening or even not there at all. Nevertheless, research of reference populations would help to shed light on genetic conditions of populations along modified river systems.

The second aspect targets the marker system. Neutral microsatellites were used to assess diversity levels as well as clonal structures. For aspects such as clonal identity, genetic drift or inbreeding these markers provide a suitable tool. However, assessing the risk that arises due to potential losses of genetic diversity on the long-term adaptation potential of species based on these markers is a problem (Ouborg *et al.* 2006). Instead, using candidate genes to assess adaptive response to environmental changes appears a promising tool (Hoffmann & Willi 2008). While research about adaptive genes is still in its infancy, studies of model organisms such as different *Populus* species, which have substantial economical importance (Sims *et al.* 2006), have already achieved some goals, e.g. in relations of potential candidate genes and drought response (Street *et al.* 2006). This information could also help to clarify relations of genetic diversity and genetic adaptive capacity in floodplain willows to finally assess potential threats of climate change from a molecular point of view.

Summarising, a lot of knowledge is already available about the ecology of riparian softwood forest species and restoration activities from that point of view feasible, though climate change displays a big and urgent, new challenge. However, societal as well as economical demands produce the strongest restrictions regarding the restoration of this invaluable vegetation type in particular and floodplains in general. Though as results of paper III demonstrated restoration of riparian softwood forests and economical/societal demands do not have to be mutually exclusive. Hence, more approaches are needed assessing the monetary value of floodplain vegetation in terms of ecosystem services (Vose et al. 2011), as simply stating that riparian softwood forests are beautiful and highly endangered seems to be not enough. In this context, research should also be conducted on ecosystem services that can be achieved by restored systems, such as plantings, which might resemble natural systems in structure but not so much in function (Mac Nally *et al.* 2010; Feld *et al.* 2011).

In general, restoration measures should be based on a sound scientific basis to increase success. Nevertheless, rigorous testing of such approaches is necessary to record and analyse if intended aims are actually accomplished (Hughes *et al.* 2005; Palmer *et al.* 2005). Given the complexity of abiotic and biotic processes in floodplain ecosystems and the remaining uncertainties of restoration measures regarding what can be achieved, “trial and error“-actions guided by a sound scientific basis and especially documenting and learning from failures to adjust measures might be the only possibility facing up to future challenges of managing river floodplain ecosystems. In this spirit, interdisciplinary projects combining the diverse aspects of river management are urgently needed.

References

Adair, R., Sagliocco, J. L., Bruzzese, E., 2006. Strategies for the biological control of invasive willows (*Salix* spp.) in Australia. Australian Journal of Entomology 45, 259-267.

Aguilar, R., Quesada, M., Ashworth, L., Herrerias-Diego, Y., Lobo, J., 2008. Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches. Molecular Ecology 17, 5177-5188.

Amlin, N. A., Rood, S. B., 2001. Inundation tolerances of riparian willows and cottonwoods. Journal of the American Water Resources Association 37, 1709-1720.

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

Amoros, C., 2001. The concept of habitat diversity between and within ecosystems applied to river side-arm restoration. Environmental Management 28, 805-817.

Andrews, D. M., Barton, C. D., Czapka, S. J., Kolka, R. K., Sweeney, B. W., 2010. Influence of tree shelters on seedling success in an afforested riparian zone. New Forests 39, 157-167.

Araujo, M. B., Guisan, A., 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography 33, 1677-1688.

Araujo, M. B., Luoto, M., 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16, 743-753.

Araujo, M. B., New, M., 2007. Ensemble forecasting of species distributions. Trends in Ecology & Evolution 22, 42-47.

Araujo, M. B., Pearson, R. G., Thuiller, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Global Change Biology 11, 1504-1513.

Araujo, M. B., Alagador, D., Cabeza, M., Nogues-Bravo, D., Thuiller, W., 2011. Climate change threatens European conservation areas. Ecology Letters 14, 484-492.

Arnaud-Haond, S., Duarte, C. M., Alberto, F., Serrao, E. A., 2007. Standardizing methods to address clonality in population studies. Molecular Ecology 16, 5115-5139.

Arnold, J. G., Allen, P. M., Bernhardt, G., 1993. A comprehensive surface-groundwater flow model. Journal of Hydrology 142, 47-69.

Auble, G. T., Scott, M. L., 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. Wetlands 18, 546-556.

Austin, M. P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological Modelling 157, 101-118.

Baptist, M. J., Penning, W. E., Duel, H., Smits, A. J. M., Geerling, G. W., van der Lee, G. E. M., Van Alphen, J. S. L., 2004. Assessment of the effects of cyclic floodplain rejuvenation on flood levels and biodiversity along the Rhine River. River Research and Applications 20, 285-297.

Barker, J. H. A., Pahlich, A., Trybush, S., Edwards, K. J., Karp, A., 2003. Microsatellite markers for diverse *Salix* species. Molecular Ecology Notes 3, 4-6.

Barsoum N., Hughes F.M.R., 1998. Regeneration response of black poplar to changing river levels. Hydrology in a Changing Environment, 1, 397–412.

Barsoum, N., 2002. Relative contributions of sexual and asexual regeneration strategies in *Populus nigra* and *Salix alba* during the first years of establishment on a braided gravel bed river. Evolutionary Ecology 15, 255-279.

Barsoum, N., Muller, E., Skot, L., 2004. Variations in levels of clonality among *Populus nigra* L. stands of different ages. Evolutionary Ecology 18, 601-624.

Bates D., Maechler M., 2010. lme4: linear mixed-effects models using S4 classes, R package, Available from http://CRAN.R-project.org/package=lme4 (accessed 02 March 2011).

Beaumont, L. J., Hughes, L., Pitman, A. J., 2008. Why is the choice of future climate scenarios for species distribution modelling important? Ecology Letters 11, 1135-1146.

Beechie, T. J., Sear, D. A., Olden, J. D., Pess, G. R., Buffington, J. M., Moir, H., Roni, P., Pollock, M. M., 2010. Process-based principles for restoring river ecosystems. Bioscience 60, 209-222.

Beffa, C., 2004. FLUMEN - User manual. www.fluvial.ch.

Beffa, C., Connell, R. J., 2001. Two-dimensional flood plain flow. I: Model description. Journal of Hydrologic Engineering 6, 397-405.

Beismann H., Barker J.H.A., Karp A., Speck T. (1997) AFLP analysis sheds light on distribution of two *Salix* species and their hybrid along a natural gradient. Molecular Ecology, 6, 989–993.

Beismann, H., Wilhelmi, H., Bailleres, H., Spatz, H. C., Bogenrieder, A., Speck, T., 2000. Brittleness of twig bases in the genus *Salix*: fracture mechanics and ecological relevance. Journal of Experimental Botany 51, 617-633.

Belcher J.W., Keddy P.A., Twolan-Strutt L. (1995) Root and shoot competition intensity along a soil depth gradient. Journal of Ecology, 83, 673–682.

Bendix, J., Hupp, C. R., 2000. Hydrological and geomorphological impacts on riparian plant communities. Hydrological Processes 14, 2977-2990.

Blom, C. W. P. M., 1999. Adaptations to flooding stress: From plant community to molecule. Plant Biology 1, 261-273.

BMU, BfN, 2009. Auenzustandsbericht - Flussauen in Deutschland. eds. N. C. a. N. S. German Federal Ministry for the Environment & German Federal Agency for Nature Conservation, Silbertal, Niestetal.

Bonn, A., Schroder, B., 2001. Habitat models and their transfer for single and multi species groups: a case study of carabids in an alluvial forest. Ecography 24, 483-496.

Booy, G., Hendriks, R. J. J., Smulders, M. J. M., Van Groenendael, J. M., Vosman, B., 2000. Genetic diversity and the survival of populations. Plant Biology 2, 379-395.

Born, C., Kjellberg, F., Chevallier, M. H., Vignes, H., Dikangadissi, J. T., Sanguie, J., Wickings, E. J., Hossaert-McKey, M., 2008. Colonization processes and the maintenance of genetic diversity: insights from a pioneer rainforest tree, *Aucoumea klaineana*. Proceedings of the Royal Society B-Biological Sciences 275, 2171-2179.

Braatne, J. H., Jamieson, R., Gill, K. M., Rood, S. B., 2007. Instream flows and the decline of riparian cottonwoods along the Yakima River, Washington, USA. River Research and Applications 23, 247-267.

Bradshaw, C. J., Sodhi, N. S., Peh, K. S., Brook, B. W., 2007. Global evidence that deforestation amplifies flood risk and severity in the developing world. Global Change Biology 13, 2379-2395.

Breckle, S. W., 2002. Walter's vegetation of the earth: the ecological systems of the geo-biosphere, 4. edn. Springer, Berlin Heidelberg.

Brose, U., Tielborger, K., 2005. Subtle differences in environmental stress along a flooding gradient affect the importance of inter-specific competition in an annual plant community. Plant Ecology 178, 51-59.

Brown, A. G., Harper, D., Peterken, G. F., 1997. European floodplain forests: structure, functioning and management. Global Ecology and Biogeography Letters 6, 169-178.

Budde, K. B., Gallo, L., Marchelli, P., Mosner, E., Liepelt, S., Ziegenhagen, B., Leyer, I., 2011. Wide spread invasion without sexual reproduction? A case study on European willows in Patagonia, Argentina. Biological Invasions 13, 45-54.

Buijse, A. D., Coops, H., Staras, M., Jans, L. H., Van Geest, G. J., Grift, R. E., Ibelings, B. W., Oosterberg, W., Roozen, F. C. J. M., 2002. Restoration strategies for river floodplains along large lowland rivers in Europe. Freshwater Biology 47, 889-907.

Casper B.B., Jackson R.B. (1997) Plant competition underground. Annual Review of Ecology and Systematics, 28, 545–570.

Chmelař J., Meusel W. (1986) Die Weiden Europas Die Gattung *Salix*. A. Ziemsen, Wittenberg, Germany.

Carvalho, S. B., Brito, J. C., Crespo, E. G., Watts, M. E., Possingham, H. P., 2011. Conservation planning under climate change: Toward accounting for uncertainty in predicted species distributions to increase confidence in conservation investments in space and time. Biological Conservation 144, 2020-2030.

Christensen, J. H., Christensen, O. B., 2003. Climate modelling: Severe summertime flooding in Europe. Nature 421, 805-806.

Cooper, D. J., Merritt, D. M., Andersen, D. C., Chimner, R. A., 1999. Factors controlling the establishment of Fremont cottonwood seedlings on the upper Green River, USA. Regulated Rivers-Research & Management 15, 419-440.

Crawley, M., 2002. Statistical Computing: An Introduction to Data Analysis Using S-Plus, 1st edn. John Wiley & Sons.

Crawley M.J. (2007) The R book. Wiley, Chichester, UK.

Dankers, R., Feyen, L., 2008. Climate change impact on flood hazard in Europe: An assessment based on high-resolution climate simulations. Journal of Geophysical Research-Atmospheres 113, 1-17.

DEWA-Europe, 2004. Freshwater in Europe - Facts, Figures and Maps. UNEP - United Nations Envoirnmental Program.

Dietrich, R. A., 2007. Fließverhalten der Elbe bei Hochwasser unter Berücksichtigung des Fließverhaltens. Wasser & Abfall 12, 20-24.

Dormann, C. F., 2007. Promising the future? Global change projections of species distributions. Basic and Applied Ecology 8, 387-397.

Dumolin, S., Demesure, B., Petit, R. J., 1995. Inheritance of chloroplast and mitochondrial genomes in pedunculate oak investigated with an efficient PCR method. Theoretical and Applied Genetics 91, 1253-1256.

Dworak, T., 2008. Flood risk management and floodplain restoration in Europe. In Restoring floodplains in Europe, eds. T. Moss & J. Monstadt, pp. 47-60. IWA Publishing, London.

Dynesius, M., Nilsson, C., 1994. Fragmentation and flow regulation of river systems in the northern 3rd of the world. Science 266, 753-762.

Elith, J., Graham, C. H., 2009. Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. Ecography 32, 66-77.

ElMousadik, A., Petit, R. J., 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L) Skeels] endemic to Morocco. Theoretical and Applied Genetics 92, 832-839.

Erwin, K. L., 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. Wetlands Ecology and Management 17, 71-84.

European Comission, 2004. Communication from the Commission to the Council, the European Parliament, the European Economic and Social Committee and the Committee of the Regions - Flood risk management - Flood prevention, protection and mitigation. - COM/2004/0472

Evanno, G., Regnaut, S., Goudet, J., 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14, 2611-2620.

Excoffier, L., Laval, G., Schneider, S., 2005. Arlequin (version 3.0): An integrated software package for population genetics data analysis. Evolutionary Bioinformatics 1, 47-50.

Feld, C. K., Birk, S., Bradley, D. C., Hering, D., Kail, J., Marzin, A., Melcher, A., Nemitz, D., Pedersen, M. L., Pletterbauer, F., Pont, D., Verdonschot, P. F., Friberg, N., 2011. From natural to degraded rivers and back again: a test of restoration ecology theory and practice.

Fielding, A. H., Bell, J. F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24, 38-49.

Foody, G. M., 2008. Refining predictions of climate change impacts on plant species distribution through the use of local statistics. Ecological Informatics 3, 228-236.

Francis, R. A., Gurnell, A. M., 2006. Initial establishment of vegetative fragments within the active zone of a braided gravel-bed river (River Tagliamento, NE Italy). Wetlands 26, 641-648.

Francis, R. A., Gurnell, A. M., Petts, G. E., Edwards, P. J., 2005. Survival and growth responses of *Populus nigra*, *Salix elaeagnos* and *Alnus incana* cuttings to varying levels of hydric stress. Forest Ecology and Management 210, 291-301.

Frankham, R., 2005. Genetics and extinction. Biological Conservation 126, 131-140.

Friedman, J. M., Scott, M. L., Lewis, W. M., 1995. Restoration of riparian forest using irrigation, artificial disturbance, and natural seedfall. Environmental Management 19, 547-557.

Geerling, G. W., Kater, E., van den Brink, C., Baptist, M. J., Ragas, A. M. J., Smits, A. J. M., 2008. Nature rehabilitation by floodplain excavation: The hydraulic effect of 16 years of sedimentation and vegetation succession along the Waal River, NL. Geomorphology 99, 317-328.

Geerling, G. W., Ragas, A. M. J., Leuven, R. S. E. W., van den Berg, J. H., Breedveld, M., Liefhebber, D., Smits, A. J. M., 2006. Succession and rejuvenation in floodplains along the river Allier (France). Hydrobiologia 565, 71-86.

Gergel, S. E., Dixon, M. D., Turner, M. G., 2002. Consequences of human-altered floods: Levees, floods, and floodplain forests along the Wisconsin River. Ecological Applications 12, 1755-1770.

Glenz, C., Schlaepfer, R., Iorgulescu, I., Kienast, F., 2006. Flooding tolerance of Central European tree and shrub species. Forest Ecology and Management 235, 1-13.

Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A. D., Aguraiuja, R., Cowell, C., Weekley, C. W., Vogg, G., Iriondo, J. M., Johnson, I., Dixon, B., Gordon, D., Magnanon, S., Valentin, B., Bjureke, K., Koopman, R., Vicens, M., Virevaire, M., Vanderborght, T., 2011. How successful are plant species reintroductions? Biological Conservation 144, 672-682.

Gonzalez, E., Gonzalez-Sanchis, M., Cabezas, A., Comin, F. A., Muller, E., 2010a. Recent Changes in the Riparian Forest of a Large Regulated Mediterranean River: Implications for Management. Environmental Management 45, 669-681.

Gonzalez, E., Gonzalez-Sanchis, M., Comin, F. A., Muller, E., 2010b. Hydrologic thresholds for riparian forest conservation in a regulated large mediterranean river. River Research and Applications 1-10.

Görgen, K., Beersma, J., Brahmer, G., Buiteveld, H., Carambia, M., de Keizer, O., Krahe, P., Nilson, E., Lammersen, R., Perrin, C., Volken, D., 2010. Assessment of climate change impacts on discharge in the Rhine River basin: results of the RheinBlick2050 Project. pp. 1-228. International Commission for the Hydrology of the Rhine Basin, Lelystad.

Goudet, J., 1995. FSTAT (Version 1.2): A computer program to calculate F-statistics. Journal of Heredity 86, 485-486.

Grime, J. P., 1979. Plant strategies and vegetation processes. - 222 S., Wiley & Sons , Chichester, New York, Brisbane, Toronto.

Grubb, P. J., 1977. Maintenance of species-richness in plant communities - importance of regeneration niche. Biological Reviews of the Cambridge Philosophical Society 52, 107-145.

Guilloy-Froget, H., Muller, E., Barsoum, N., Hughes, F. M. R., 2002. Dispersal, germination, and survival of *Populus nigra* L. (Salicaceae) in changing hydrologic conditions. Wetlands 22, 478-488.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8, 993-1009.

Guisan, A., Zimmermann, N. E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147-186.

Gurevitch J., Scheiner S.M., Fox G.A. (2006) The ecology of plants, 2nd edition. Sinauer Associates Inc., Sunderland, MA.

Gurnell, A., 1997. The hydrological and geomorphological significance of forested floodplains. Global Ecology and Biogeography 6, 219-229.

Gurnell, A., Petts, G., 2006. Trees as riparian engineers: the Tagliamento River, Italy. Earth Surface Processes and Landforms 31, 1558-1574.

Hager H., Schume H. (2000) The floodplain forests along the Austrian Danube. In: Klimo E.H., Hager H. (Eds), The floodplain forests in Europe: current situation and perspectives. Brill Academic Publishers, Leyden, Germany, pp 83–100.

Hanley, S., Barker, J. H. A., Van Ooijen, J. W., Aldam, C., Harris, S. L., Ahman, I., Larsson, S., Karp, A., 2002. A genetic linkage map of willow (*Salix viminalis*) based on AFLP and microsatellite markers. Theoretical and Applied Genetics 105, 1087-1096.

Hardy, O. J., Vekemans, X., 2002. SPAGEDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Molecular Ecology Notes 2, 618-620.

Harper, D., Witkowski, F., KempMcCarthy, D., Crabb, J., 1997. The distribution and abundance of riparian trees in English lowland floodplains. Global Ecology and Biogeography Letters 6, 297-306.

Harrell, F. E., 2001. Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis, Springer, New York.

Hattermann, F., Conradt, T., Bronstert, A., 2007. Berechnung großskaliger Verdunstung unter den Bedingungen des globalen Wandels. Forum für Hydrologie und Wasserbewirtschaftung 21, 231-247.

Heikkinen, R. K., Luoto, M., Araujo, M. B., Virkkala, R., Thuiller, W., Sykes, M. T., 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30, 751-777.

Henderson, L., 1992. Invasive alien woody plants of the Eastern Cape. Bothalia 22, 119-143.

Hering, D., Borja, A., Carstensen, J., Carvalho, L., Elliott, M., Feld, C. K., Heiskanen, A. S., Johnson, R. K., Moe, J., Pont, D., Solheim, A. L., van de Bund, W., 2010. The European Water Framework Directive at the age of 10: a critical review of the achievements with recommendations for the future. Science of the Total Environment 408, 4007-4019.

Hirzel, A., Guisan, A., 2002. Which is the optimal sampling strategy for habitat suitability modelling. Ecological Modelling 157, 331-341.

Hirzel, A. H., Le Lay, G., 2008. Habitat suitability modelling and niche theory. Journal of Applied Ecology 45, 1372-1381.

Hoffmann, A. A., Willi, Y., 2008. Detecting genetic responses to environmental change. Nature Reviews Genetics 9, 421-432.

Horritt, M., Bates, P., Mattinson, M., 2006. Effects of mesh resolution and topographic representation in 2D finite volume models of shallow water fluvial flow. Journal of Hydrology 329, 306-314.

Hoshikawa, T., Kikuchi, S., Nagamitsu, T., Tomaru, N., 2009. Eighteen microsatellite loci in *Salix arbutifolia* (Salicaceae) and cross-species amplification in *Salix* and *Populus* species. Molecular Ecology Resources 9, 1202-1205.

Hothorn T., Bretz F., Westfall P. (2008) Simultaneous inference in general parametric models. Biometrical Journal, 50, 346–363.

Hosmer, D. W., Lemeshow, S., 2000. Applied logistic regression, 2nd edn. Wiley, New York.

Hughes, F. M. R., 1997. Floodplain biogeomorphology. Progress in Physical Geography 21, 501-529.

Hughes, F. M. R., Adams, W. M., Muller, E., Nilsson, C., Richards, K. S., Barsoum, N., Decamps, H., Foussadier, R., Girel, J., Guilloy, H., Hayes, A., Johansson, M., Lambs, L., Pautou, G., Peiry, J. L., Perrow, M., Vautier, F., Winfield, M., 2001. The importance of different scale processes for the restoration of floodplain woodlands. Regulated Rivers-Research & Management 17, 325-345.

Hughes, F. M. R., Barsoum, N., Richards, K. S., Winfield, M., Hayes, A., 2000. The response of male and female black poplar (*Populus nigra* L. subspecies *betulifolia* (Pursh) W. Wettst,) cuttings to different water table depths and sediment types: implications for flow management and river corridor biodiversity. Hydrological Processes 14, 3075-3098.

Hughes, F. M. R., Colston, A., Mountford, J. O., 2005. Restoring riparian ecosystems: The challenge of accommodating variability and designing restoration trajectories. Ecology and Society 10.

Hughes, F. M. R., Rood, S. B., 2003. Allocation of river flows for restoration of floodplain forest ecosystems: A review of approaches and their applicability in Europe. Environmental Management 32, 12-33.

Hunter J.C., Willett K.B., McCoy M.C., Quinn J.F., Keller K.E. (1999) Prospects for preservation and restoration of riparian forests in the Sacramento Valley, California, USA. Environmental Management, 24, 65–75.

IKSE, 2005. Die Elbe und ihr Einzugsgebiet - Ein geographisch-hydrologischer und wasserwirtschaftlicher Überblick. IKSE - Internationale Kommission zum Schutz der Elbe, Magdeburg.

Ilg, C., Dziock, F., Foeckler, F., Follner, K., Gerisch, M., Glaeser, J., Rink, A., Schanowski, A., Scholz, M., Deichner, O., Henle, K., 2008. Long-term reactions of plants and macroinvertebrates to extreme floods in floodplain grasslands. Ecology 89, 2392-2398.

Imbert, E., Lefevre, F., 2003. Dispersal and gene flow of *Populus nigra* (Salicaceae) along a dynamic river system. Journal of Ecology 91, 447-456.

IPCC, 2007. Climate Change 2007: Synthesis Report (AR4) - Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. eds. R. Pachauri & A. Reisinger, IPCC, Geneva, Switzerland.

Jacquemyn, H., Honnay, O., Van Looy, K., Breyne, P., 2006. Spatiotemporal structure of genetic variation of a spreading plant metapopulation on dynamic riverbanks along the Meuse River. Heredity 96, 471-478.

Järvelä, J., 2002. Flow resistance of flexible and stiff vegetation: a flume study with natural plants. Journal of Hydrology 269, 44-54.

Jensen, K., Trepel, M., Merritt, D., Rosenthal, G., 2006. Restoration ecology of river valleys. Basic and Applied Ecology 7, 383-387.

Johnson, W. C., 2000. Tree recruitment and survival in rivers: influence of hydrological processes. Hydrological Processes 14, 3051-3074.

Jung, V., Mony, C., Hoffmann, L., Muller, S., 2009. Impact of competition on plant performances along a flooding gradient: a multi-species experiment. Journal of Vegetation Science 20, 433-441.

Karrenberg, S., Edwards, P. J., Kollmann, J., 2002. The life history of Salicaceae living in the active zone of floodplains. Freshwater Biology 47, 733-748.

Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12, 334-350.

Kehl, A., Reuter, A., Aas.G., 2008. Relevance of phenology of seed dispersal and water level on the establishment of seedlings of different *Salix*-species on restored river sites. Tuexenia 28, 85-101.

Keith, D. A., Akcakaya, H. R., Thuiller, W., Midgley, G. F., Pearson, R. G., Phillips, S. J., Regan, H. M., Araujo, M. B., Rebelo, T. G., 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. Biology Letters 4, 560-563.

Kondolf, G. M., Piegay, H., Landon, N., 2007. Changes in the riparian zone of the lower Eygues River, France, since 1830. Landscape Ecology 22, 367-384.

Korn, N., Jessel, B., Hasch, B., Mühlinghaus, R., 2005. Flussauen und Wasserrahmenrichtlinie. Bedeutung der Flussauen für die Umsetzung der europäischen Wasserrahmenrichtlinie - Handlungsempfehlungen für Naturschutz und Wasserwirtschaft., Landwirtschaftsverlag GmbH, Münster.

Kotowski, W., Beauchard, O., Opdekamp, W., Meire, P., van Diggelen, R., 2010. Waterlogging and canopy interact to control species recruitment in floodplains. Functional Ecology 24, 918-926.

Kramer, A. T., Ison, J. L., Ashley, M. V., Howe, H. F., 2008a. The paradox of forest fragmentation genetics. Conservation Biology 22, 878-885.

Kramer, K., Vreugdenhil, S. J., van der Werf, D. C., 2008b. Effects of flooding on the recruitment, damage and mortality of riparian tree species: A field and simulation study on the Rhine floodplain. Forest Ecology and Management 255, 3893-3903.

Krysanova, V., Meiner, A., Roosaare, J., Vasilyev, A., 1989. Simulation Modeling of the Coastal Waters Pollution from Agricultural Watershed. Ecological Modelling 49, 7-29.

Krysanova, V., Muller-Wohlfeil, D. I., Becker, A., 1998. Development and test of a spatially distributed hydrological water quality model for mesoscale watersheds. Ecological Modelling 106, 261-289.

Kundzewicz, Z. W., Lugeri, N., Dankers, R., Hirabayashi, Y., Doll, P., Pinskwar, I., Dysarz, T., Hochrainer, S., Matczak, P., 2010. Assessing river flood risk and adaptation in Europe - review of projections for the future. Mitigation and Adaptation Strategies for Global Change 15, 641-656.

Lautenschlager E. (1994) Weiden von Mittel- und Nordeuropa. Birkhauser Verlag, Basel, Swirtzerland.

Lenssen, J. P. M., Menting, F. B. J., Van der Putten, W. H., 2003. Plant responses to simultaneous stress of waterlogging and shade: amplified or hierarchical effects? New Phytologist 157, 281-290.

Leyer, I., 2004. Effects of dykes on plant species composition in a large lowland river floodplain. River Research and Applications 20, 813-827.

Leyer, I., 2005. Predicting plant species' responses to river regulation: the role of water level fluctuations. Journal of Applied Ecology 42, 239-250.

Leyer, I., Mosner, E., Lehmann, B., 2012. Managing floodplain forest restoration in European river landscapes combining ecological and flood protection issues. Ecological Applications 22, 240-249.

Leyer, I., 2006. Dispersal, diversity and distribution patterns in pioneer vegetation: The role of river-floodplain connectivity. Journal of Vegetation Science 17, 407-416.

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

Liu, C. R., Berry, P. M., Dawson, T. P., Pearson, R. G., 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385-393.

Loiselle, B. A., Sork, V. L., Nason, J., Graham, C., 1995. Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (Rubiaceae). American Journal of Botany 82, 1420-1425.

Lytle, D. A., Poff, N. L., 2004. Adaptation to natural flow regimes. Trends in Ecology & Evolution 19, 94-100.

Mac Nally, R., De Vries, L., Thomson, J. R., 2010. Are Replanted Floodplain Forests in Southeastern Australia Providing Bird Biodiversity Benefits? Restoration Ecology 18, 85-94.

Mahoney, J. M., Rood, S. B., 1998. Streamflow requirements for cottonwood seedling recruitment - An interactive model. Wetlands 18, 634-645.

May, S. E., Medley, K. A., Johnson, S. A., Hoffman, E. A., 2011. Combining genetic structure and ecological niche modeling to establish units of conservation: a case study of an imperiled salamander. Biological Conservation 144, 1441-1450.

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

Moggridge, H. L., Gurnell, A. M., 2009. Controls on the sexual and asexual regeneration of Salicaceae along a highly dynamic, braided river system. Aquatic Sciences 71, 305-317.

Monstadt, J., 2008. The relocation of a dyke on the River Elbe: floodplain management as a challenge for intersectoral and multilevel coordination. In Restoring floodplains in Europe, eds. T. Moss & J. Monstadt, pp. 229-260. IWA Publishing, London.

Montenegro, H., Holfelder, T. W. B., 1999. Untersuchung der Wechselwirkung zwischen Oberflächengewässer und Grundwasser in Flussauen. Auenreport Sonderband 1, 27-40.

Mosner, E., Schneider, S., Lehmann, B., Leyer, I., 2011. Hydrological prerequisites for optimum habitats of riparian *Salix* communities – identifying suitable reforestation sites. Applied Vegetation Science 14, 367-377.

Munzel, U., Hothorn, L. A., 2001. A unified approach to simultaneous rank test procedures in the unbalanced one-way layout. Biometrical Journal 43, 553-569.

Nagelkerke, N. J. D., 1991. A note on a general definition of the coefficient of determination. Biometrika 78, 691-692.

Naiman, R. J., Decamps, H., 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28, 621-658.

Nakamura, F., Shin, N., Inahara, S., 2007. Shifting mosaic in maintaining diversity of floodplain tree species in the northern temperate zone of Japan. Forest Ecology and Management 241, 28-38.

Nestmann, F., Büchele, B., 2002. Morphodynamik der Elbe - Schlussbericht des BMBF-Verbundprojektes mit Einzelbeiträgen der Partner und Anlagen-CD, Institut für Wasserwirtschaft und Kulturtechnik, Universität Karlsruhe (TH).

Nicholas, A. P., Mitchell, C. A., 2003. Numerical simulation of overbank processes in topographically complex floodplain environments. Hydrological Processes 17, 727-746.

Nilsson, C., Berggren, K., 2000. Alterations of riparian ecosystems caused by river regulation. Bioscience 50, 783-792.

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

Nilsson, C., Jansson, R., Malmqvist, B., Naiman, R. J., 2007. Restoring riverine landscapes: The challenge of identifying priorities, reference states, and techniques. Ecology and Society 12.

Nilsson, C., Svedmark, M., 2002. Basic principles and ecological consequences of changing water regimes: Riparian plant communities. Environmental Management 30, 468-480.

Opperman, J. J., Luster, R., McKenney, B. A., Roberts, M., Meadows, A. W., 2010. Ecologically Functional Floodplains: Connectivity, Flow Regime, and Scale1. JAWRA Journal of the American Water Resources Association 46, 211-226.

Orlowsky, B., Gerstengarbe, F. W., Werner, P. C., 2008. A resampling scheme for regional climate simulations and its performance compared to a dynamical RCM. Theoretical and Applied Climatology 92, 209-223.

Ouborg, N. J., Vergeer, P., Mix, C., 2006. The rough edges of the conservation genetics paradigm for plants. Journal of Ecology 94, 1233-1248.

Palmer, M. A., Bernhardt, E. S., Allan, J. D., Lake, P. S., Alexander, G., Brooks, S., Carr, J., Clayton, S., Dahm, C. N., Shah, J. F., Galat, D. L., Loss, S. G., Goodwin, P., Hart, D. D., Hassett, B., Jenkinson, R., Kondolf, G. M., Lave, R., Meyer, J. L., O'Donnell, T. K., Pagano, L., Sudduth, E., 2005. Standards for ecologically successful river restoration. Journal of Applied Ecology 42, 208-217.

Palmer, M. A., Lettenmaier, D. P., Poff, N. L., Postel, S. L., Richter, B., Warner, R., 2009. Climate Change and River Ecosystems: Protection and Adaptation Options. Environmental Management 44, 1053-1068.

Palmer, M. A., Liermann, C. A. R., Nilsson, C., Florke, M., Alcamo, J., Lake, P. S., Bond, N., 2008. Climate change and the world's river basins: anticipating management options. Frontiers in Ecology and the Environment 6, 81-89.

Pautasso, M., 2009. Geographical genetics and the conservation of forest trees. Perspectives in Plant Ecology Evolution and Systematics 11, 157-189.

Peakall, R., Smouse, P. E., 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6, 288-295.

Pearce, J., Ferrier, S., 2000. Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133, 225-245.

Pearce, J., Ferrier, S., Scotts, D., 2001. An evaluation of the predictive performance of distributional models for flora and fauna in north-east New South Wales. Journal of Environmental Management 62, 171-184.

Pearman, P. B., Guisan, A., Broennimann, O., Randin, C. F., 2008. Niche dynamics in space and time. Trends in Ecology & Evolution 23, 149-158.

Pearson, R. G., Thuiller, W., Araujo, M. B., Martinez-Meyer, E., Brotons, L., McClean, C., Miles, L., Segurado, P., Dawson, T. P., Lees, D. C., 2006. Model-based uncertainty in species range prediction. Journal of Biogeography 33, 1704-1711.

Peters, J., De Baets, B., Samson, R., Verhoest, N. E. C., 2008. Modelling groundwater-dependent vegetation patterns using ensemble learning. Hydrology and Earth System Sciences 12, 603-613.

Petts, G. E., 1989. Historical change of large alluvial rivers, 1. edn. John Wiley & Sons.

Pompe, S., Hanspach, J., Badeck, F., Klotz, S., Thuiller, W., Kuhn, I., 2008. Climate and land use change impacts on plant distributions in Germany. Biology Letters 4, 564-567.

Pospiskova, M., Salkova, I., 2006. Population structure and parentage analysis of black poplar along the Morava River. Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere 36, 1067-1076.

Pritchard, J. K., Stephens, M., Donnelly, P., 2000. Inference of population structure using multilocus genotype data. Genetics 155, 945-959.

R Development Core Team, 2008. R: A language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria.

Radtke, A., Mosner, E., Leyer, I., 2012. Vegetative reproduction capacities of floodplain willows – cutting response to competition and biomass loss. Plant Biology 14, 257-264.

Randin, C. F., Dirnbock, T., Dullinger, S., Zimmermann, N. E., Zappa, M., Guisan, A., 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography 33, 1689-1703.

Randin, C. F., Engler, R., Normand, S., Zappa, M., Zimmermann, N. E., Pearman, P. B., Vittoz, P., Thuiller, W., Guisan, A., 2009. Climate change and plant distribution: local models predict high-elevation persistence. Global Change Biology 15, 1557-1569.

Rathmacher, G., Niggemann, M., Kohnen, M., Ziegenhagen, B., Bialozyt, R., 2010. Short-distance gene flow in *Populus nigra* L. accounts for small-scale spatial genetic structures: implications for in situ conservation measures. Conservation Genetics 11, 1327-1338.

Richards, K., Brasington, J., Hughes, F., 2002. Geomorphic dynamics of floodplains: ecological implications and a potential modelling strategy. Freshwater Biology 47, 559-579.

Robinson, M., Cognard-Plancq, A. L., Cosandey, C., David, J., Durand, P., Fuhrer, H. W., Hall, R., Hendriques, M. O., Marc, V., McCarthy, R., McDonnell, M., Martin, C., Nisbet, T., O'Dea, P., Rodgers, M., Zollner, A., 2003. Studies of the impact of forests on peak flows and baseflows: a European perspective. Forest Ecology and Management 186, 85-97.

Rodriguez, J. P., Brotons, L., Bustamante, J., Seoane, J., 2007. The application of predictive modelling of species distribution to biodiversity conservation. Diversity and Distributions 13, 243-251.

Roeckner, E., Arpe, K., Bengtsson, L., Christoph, M., Claussen, M., Dümenil, L., Esch, M., Giorgetta, M., Schlese, U., Schulzweida, U., 1996. The athmospheric general circulation model ECHAM-4: model descritption and simulation of present-day climate. Max-Planck-Institute, Hamburg, Germany.

Rohde, S., Hostmann, M., Peter, A., Ewald, K., 2006. Room for rivers: An integrative search strategy for floodplain restoration. Landscape and Urban Planning 78, 50-70.

Romano, S. P., 2010. Our current understanding of the Upper Mississippi River System floodplain forest. Hydrobiologia 640, 115-124.

Rood S., Mahoney J. (1990) Collapse of riparian poplar forests downstream from dams in western prairies: probable causes and prospects for mitigation. Environmental Management, 14, 451–464.

Rood, S. B., Gourley, C. R., Ammon, E. M., Heki, L. G., Klotz, J. R., Morrison, M. L., Mosley, D., Scoppettone, G. G., Swanson, S., Wagner, P. L., 2003a. Flows for floodplain forests: A successful riparian restoration. Bioscience 53, 647-656.

Rood, S. B., Kalischuk, A. R., Polzin, M. L., Braatne, J. H., 2003b. Branch propagation, not cladoptosis, permits dispersive, clonal reproduction of riparian cottonwoods. Forest Ecology and Management 186, 227-242.

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

Schaff S.D., Pezeshki S.R., Shields F.D. (2002) Effects of pre-planting soaking on growth and survival of black willow cuttings. Restoration Ecology, 10, 267–274.

Schiechtl H.M. (1992) Weiden in der Praxis: Die Weiden Mitteleuropas, ihre Verwendung und ihre Bestimmung. Patzer Verlag, Berlin, Germany.

Schier G.A., Campbell R.B. (1976) Differences among *Populus* species in ability to form adventitious shoots and roots. Canadian Journal of Forest Research, 6, 253–261.

Scott M.L., Auble G.T., Friedman J.M. (1997) Flood dependency of cottonwood establishment along the Missouri River, Montana, USA. Ecological Applications, 7, 677–690.

Schneider, S., 2010. Widerstandsverhalten von holzigen Auenpflanzen - Konzept zur Etablierung von Weichholzauen an Fließgewässern. Doktorarbeit. Universität of Karlsruhe.

Schnitzler, A., 1995. Successional status of trees in gallery forest along the River Rhine. Journal of Vegetation Science 6, 479-486.

Schnitzler, A., Hale, B. W., Alsum, E., 2005. Biodiversity of floodplain forests in Europe and eastern North America: a comparative study of the Rhine and Mississippi Valleys. Biodiversity and Conservation 14, 97-117.

Scholten, M., Anlauf, A., Büchele, B., Faulhaber, P., Henle, K., Kofalk, S., Leyer, I., Meyerhoff, J., Purps, J., Rast, G., Scholz, M., 2005. The River Elbe in Germany - present state, conflicting goals, and perspectives of rehabilitation. Large Rivers 15, 579-602.

Scholz, M., Stab, S., Dziock, F., Henle, K., 2004. Lebensräume der Elbe und ihrer Auen, Weißensee Verlag, Berlin.

Schulz, S., Baron, A., 2005. The realization of the European Water Framework Directive in the German part of the catchment area of the Elbe River. Holz und Forst 60, 307-310.

Schwartz, R., Gröngroft, A., Miehlich, G., 2003. Pore water composition as explanatory device for origin and flow direction of soil water in alluvial soils of the Middle Elbe. Acta hydrochemica et hydrobiologica 31, 423-435.

Scott, M. L., Friedman, J. M., Auble, G. T., 1996. Fluvial process and the establishment of bottomland trees. Geomorphology 14, 327-339.

Shafroth, P. B., Stromberg, J. C., Patten, D. T., 2000. Woody riparian vegetation response to different alluvial water table regimes. Western North American Naturalist 60, 66-76.

Shewchuk, J. R., 1995. Triangle: Engineering a 2D quality mesh generator and Delaunay Triangulator, Carnegie Mellon University, Pittsburgh, Pennsylvania.

Silvertown, J., 2008. The evolutionary maintenance of sexual reproduction: Evidence from the ecological distribution of asexual reproduction in clonal plants. International Journal of Plant Sciences 169, 157-168.

Sims, R. E. H., Hastings, A., Schlamadinger, B., Taylor, G., Smith, P., 2006. Energy crops: current status and future prospects. Global Change Biology 12, 2054-2076.

Skvortsov A.K., 1999. Willows of Russia and adjacent countries: taxonomical and geographical revision (translated from: Skvortsov A.K. (1968) Willows of the USSR. Taxonomic and geographic Rrevision. Nauka, Moscow), Joensuu University, Joensuu.

Slavov, G. T., Leonardi, S., Adams, W. T., Strauss, S. H., DiFazio, S. P., 2010. Population substructure in continuous and fragmented stands of *Populus trichocarpa*. Heredity 105, 348-357.

Smulders, M. J. M., Cottrell, J. E., Lefevre, F., van der Schoot, J., Arens, P., Vosman, B., Tabbener, H. E., Grassi, F., Fossati, T., Castiglione, S., Krystufek, V., Fluch, S., Burg, K., Vornam, B., Pohl, A., Gebhardt, K., Alba, N., Agundez, D., Maestro, C., Notivol, E., Volosyanchuk, R., Pospiskova, M., Bordacs, S., Bovenschen, J., van Dam, B. C., Koelewijn, H. P., Halfmaerten, D., Ivens, B., Van Slycken, J., Broeck, A. V., Storme, V., Boerjan, W., 2008. Structure of the genetic diversity in black poplar (*Populus nigra* L.) populations across European river systems: Consequences for conservation and restoration. Forest Ecology and Management 255, 1388-1399.

Stanturf, J. A., Schoenholtz, S. H., Schweitzer, C. J., Shepard, J. P., 2001. Achieving restoration success: Myths in bottomland hardwood forests. Restoration Ecology 9, 189-200.

Steffan-Dewenter, I., Tscharntke, T., 1999. Effects of habitat isolation on pollinator communities and seed set. Oecologia 121, 432-440.

Steiger, J., Gurnell, A. M., Goodson, J. M., 2003. Quantifying and characterizing contemporary riparian sedimentation. River Research and Applications 19, 335-352.

Steiger, J., James, M., Gazelle, F., 1998. Channelization and consequences on floodplain system functioning on the Garonne River, SW France. Regulated Rivers-Research & Management 14, 13-23.

Steiger, J., Tabacchi, E., Dufour, S., Corenblit, D., Peiry, J. L., 2005. Hydrogeomorphic processes affecting riparian habitat within alluvial channel-floodplain river systems: A review for the temperate zone. River Research and Applications 21, 719-737.

Stella, J., Hayden, M., Battles, J., Piegay, H., Dufour, S., Fremier, A. K., 2011. The role of abandoned channels as refugia for sustaining pioneer riparian forest ecosystems. Ecosystems 14, 776-790.

Storme, V., Vanden Broeck, A., Ivens, B., Halfmaerten, D., Van Slycken, J., Castiglione, S., Grassi, F., Fossati, T., Cottrell, J. E., Tabbener, H. E., Lefevre, F., Saintagne, C., Fluch, S., Krystufek, V., Burg, K., Bordacs, S., Borovics, A., Gebhardt, K., Vornam, B., Pohl, A., Alba, N., Agundez, D., Maestro, C., Notivol, E., Bovenschen, J., van Dam, B. C., van der Schoot, J., Vosman, B., Boerjan, W., Smulders, M. J. M., 2004. Ex-situ conservation of Black poplar in Europe: genetic diversity in nine gene bank collections and their value for nature development. Theoretical and Applied Genetics 108, 969-981.

Street, N. R., Skogstrom, O., Sjodin, A., Tucker, J., Rodriguez-Acosta, M., Nilsson, P., Jansson, S., Taylor, G., 2006. The genetics and genomics of the drought response in *Populus*. Plant Journal 48, 321-341.

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

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

Stromberg, J. C., Tluczek, M. G. F., Hazelton, A. F., Ajami, H., 2010. A century of riparian forest expansion following extreme disturbance: Spatio-temporal change in *Populus/Salix/Tamarix* forests along the Upper San Pedro River, Arizona, USA. Forest Ecology and Management 259, 1181-1189.

Sweeney, B. W., Bott, T. L., Jackson, J. K., Kaplan, L. A., Newbold, J. D., Standley, L. J., Hession, W. C., Horwitz, R. J., 2004. Riparian deforestation, stream narrowing, and loss of stream ecosystem services. Proceedings of the National Academy of Sciences of the United States of America 101, 14132-14137.

Talbot, J., Richard, P. J. H., Roulet, N. T., Booth, R. K., 2010. Assessing long-term hydrological and ecological responses to drainage in a raised bog using paleoecology and a hydrosequence. Journal of Vegetation Science 21, 143-156.

Thomas, H., Nisbet, T. R., 2007. An assessment of the impact of floodplain woodland on flood flows. Water and Environment Journal 21, 114-126.

Thuiller, W., Lavorel, S., Araujo, M. B., Sykes, M. T., Prentice, I. C., 2005. Climate change threats to plant diversity in Europe. Proceedings of the National Academy of Sciences of the United States of America 102, 8245-8250.

Tockner, K., Robinson, C. T., Uehlinger, U., 2009. Rivers of Europe, 1st edn. Elsevier, London.

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

Toogood, S. E., Joyce, C. B., 2009. Effects of raised water levels on wet grassland plant communities. Applied Vegetation Science 12, 283-294.

Trivedi, M. R., Berry, P. M., Morecroft, M. D., Dawson, T. P., 2008. Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. Global Change Biology 14, 1089-1103.

Trung L.Q., Van Puyvelde K., Triest L. (2008) Consensus primers of cyp73 genes discriminate willow species and hybrids (*Salix*, Salicaceae). Molecular Ecology Resources, 8, 455–458.

Twolan-Strutt L., Keddy P.A. (1996) Above- and belowground competition intensity in two contrasting wetland plant communities. Ecology, 77, 259–270.

UNEP-WCMC, 2000. European forests and protected areas: Gap analysis. United Nations Environmental Program - World Conservation Monitoring Centre, Cambridge, UK.

van Coller, A. L., Rogers, K. H., Heritage, G. L., 2000. Riparian vegetation-environment relationships: complimentarity of gradients versus patch hierarchy approaches. Journal of Vegetation Science 11, 337-350.

van Dijk, A. I. J. M., Keenan, R. J., 2007. Planted forests and water in perspective. Forest Ecology and Management 251, 1-9.

Van Eck, W. H. J. M., van de Steeg, H. M., Blom, C. W. P. M., de Kroon, H., 2004. Is tolerance to summer flooding correlated with distribution patterns in river floodplains? A comparative study of 20 terrestrial grassland species. Oikos 107, 393-405.

Van Eck, W. H. J. M., van de Steeg, H. M., Blom, C. W. P. M., de Kroon, H., 2005. Recruitment limitation along disturbance gradients in river floodplains. Journal of Vegetation Science 16, 103-110.

Van Looy, K., Honnay, O., Bossuyt, B., Hermy, M., 2004. The effects of river embankment and forest fragmentation on the plant species richness and composition of floodplain forests in the Meuse Valley, Belgium. Belgian Journal of Botany 136, 97-108.

Van Looy, K., Jacquemyn, H., Breyne, P., Honnay, O., 2009. Effects of flood events on the genetic structure of riparian populations of the grassland plant *Origanum vulgare*. Biological Conservation 142, 870-878.

Van Splunder, I., Coops, H., Voesenek, L. A. C. J., Blom, C. W. P. M., 1995. Establishment of alluvial forest species in floodplains - the role of dispersal timing, germination characteristics and water-level fluctuations. Acta Botanica Neerlandica 44, 269-278.

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

van Stokkom, H. T. C., Smits, A. J. M., Leuven, R. S. E. W., 2005. Flood defense in the Netherlands - A new era, a new approach. Water International 30, 76-87.

Vaughan, I. P., Ormerod, S. J., 2005. The continuing challenges of testing species distribution models. Journal of Applied Ecology 42, 720-730.

Vekemans, X., Hardy, O. J., 2004. New insights from fine-scale spatial genetic structure analyses in plant populations. Molecular Ecology 13, 921-935.

Vreugdenhil, S. J., Kramer, K., Pelsma, T., 2006. Effects of flooding duration, -frequency and -depth on the presence of saplings of six woody species in north-west Europe. Forest Ecology and Management 236, 47-55.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389-395.

Ward, J. V., Tockner, K., 2001. Biodiversity: towards a unifying theme for river ecology. Freshwater Biology 46, 807-819.

Ward, J. V., Tockner, K., Arscott, D. B., Claret, C., 2002. Riverine landscape diversity. Freshwater Biology 47, 517-539.

Ward, J. V., Tockner, K., Schiemer, F., 1999. Biodiversity of floodplain river ecosystems: Ecotones and connectivity. Regulated Rivers-Research & Management 15, 125-139.

Watkinson, A. R., Powell, J. C., 1993. Seedling recruitment and the maintenance of clonal diversity in plant-populations - A computer-simulation of *Ranunculus repens*. Journal of Ecology 81, 707-717.

Watson, E. B., Byrne, R., 2009. Abundance and diversity of tidal marsh plants along the salinity gradient of the San Francisco Estuary: implications for global change ecology. Plant Ecology 205, 113-128.

Weir, B. S., Cockerham, C. C., 1984. Estimating F-statistics for the analysis of population-structure. Evolution 38, 1358-1370.

White, J. M., Stromberg, J. C., 2011. Resilience, restoration, and riparian ecosystems: Case study of a dry land, urban river. Restoration Ecology 19, 101-111.

Winfield, M., Hughes, F. M. R., 2002. Variation in *Populus nigra* clones: Implications for river restoration projects in the United Kingdom. Wetlands 22, 33-48.

Ziegenhagen, B., Gneuss, S., Rathmacher, G., Leyer, I., Bialozyt, R., Heinze, B., Liepelt, S., 2008. A fast and simple genetic survey reveals the spread of poplar hybrids at a natural Elbe river site. Conservation Genetics 9, 373-379.

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List of publications

Peer-reviewed

Leyer, I., **Mosner, E.** & Lehmann, B. (2012) Managing floodplain forest restoration in European river landscapes combining ecological and flood protection issues. Ecological Applications 22, 240 – 249.

Radtke, A., **Mosner, E.** & Leyer, I. (2011) Vegetative reproduction capacities of floodplain willows – cutting response to competition and biomass loss. Plant Biology 14, 257 – 264.

Blaum, N., **Mosner, E.**, Schwager, M. & Jeltsch, F. (2011) How functional is functional? Ecological groupings in terrestrial animal ecology: towards an animal functional type approach. Biodiversity and Conservation 20, 2333 – 2345.

Mosner, E., Schneider, S., Lehmann, B. & Leyer, I. (2011) Hydrological prerequisites for optimum habitats of riparian *Salix* communities – identifying suitable reforestation sites. Applied Vegetation Science 14, 367 – 377.

Budde, K.B., Gallo, L., Marchelli, P, **Mosner, E.**, Liepelt, S, Ziegenhagen, B, Leyer, I. (2011) Wide spread invasion without sexual reproduction? A case study on European willows in Patagonia, Argentina. Biological Invasions 13, 45 – 54.

Enright, N.J., **Mosner, E.**, Miller, B.P., Johnson, N., Lamont, B.B. (2007) Soil vs. canopy seed storage and plant species coexistence in species-rich Australian shrublands. Ecology 88, 2292 – 2304.

Others

Mosner, E., Leyer, I., Schneider, S., Lehmann, B., Galonska, H. (2010) Praxisleitfaden zur Weichholzauenetablierung an Bundeswasserstraßen – Ein Beitrag zum naturverträglichen Hochwasserschutz. http://www.uni-marburg.de/fb17/fachgebiete/naturschutz/naturschutzbiologie/praxis/leitfadenkoweb.pdf

Mosner, E., Schneider, S., Lehmann, B. & Leyer, I. (2009) Weichholzauen-Entwicklung als Beitrag zum naturverträglichen Hochwasserschutz im Biosphärenreservat Mittelelbe. Naturschutz im Land Sachsen-Anhalt, Sonderheft 46. Jahrgang, 29 – 40.

Mosner, E., Schneider, S., Conradt, T., Lehmann, B., Hattermann, F.F. & Leyer, I. (2008) Floodplain forests and climate change – current state and future patterns. Extended Abstract, 6th European Conference on Ecological Restoration, Ghent/Belgium.

Schneider, S., **Mosner, E.**, Leyer, I. & Lehmann, B. (2006) Weichholzauen-Etablierung an der Elbe. Forum Geoökologie 17, 20 – 23.

Erklärung

Hiermit versichere ich, dass ich meine Dissertation

**„Habitat distribution and population genetics of riparian *Salix* species in space and time –
a restoration framework for softwood forests along the Elbe River"**

selbständig und ohne fremde Hilfe angefertigt habe und mich keiner als der von mir ausdrücklich bezeichneten Quellen und Hilfen bedient habe. Alle vollständig oder sinngemäß übernommenen Zitate habe ich als solche gekennzeichnet. Diese Dissertation wurde in der jetzigen oder einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Marburg /Lahn, November 2011