Possible effects of climate change on the vegetation of floodplain meadows

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„Mir ist noch keine komplizierte Frage begegnet, die bei richtiger Betrachtung nicht noch komplizierter geworden wäre“

- nach Poul Anderson -

CONTENTS

CHAPTER 1

THE DYNAMIC ECOSYSTEM OF FLOODPLAIN MEADOWS AND FUTURE IMPACTS DUE TO CLIMATE CHANGE – INTRODUCTION

Kristin Ludewig

Floodplain meadows

Floodplains are dynamic and productive ecosystems with diverse plant and animal communities and are considered hot spots of biodiversity (Naiman, Décamps & Pollock 1993; Naiman & Décamps 1997; Tockner & Stanford 2002). Rather formally, floodplains are defined as Holocene alluvial lowlands along large and small rivers (Ad-hoc-AG-Boden 2005). As the name already suggests, floodplains are characterized by the occurrence of flooding events, which are a strong driver for all processes in floodplain ecosystems. Flooding causes, for example, erosion and sedimentation (Krüger *et al.* 2006), temporarily anaerobic soil conditions (Langer & Rinklebe 2009) and affects the nutrient regime of the floodplain (Beltman, Willems & Güsewell 2007). Due to the impact of flooding events mainly in winter and spring, in combination with dry conditions over the summer, floodplains are highly dynamic environments (Hölzel & Otte 2001). Overall, the soil water potentials are not only variable along flooding gradients, but also within and between years. This variability might be one of the most striking characteristics of floodplain ecosystems.

Generally, floodplains fulfill many functions (e.g. Schindler et al. 2014). For instance, they attenuate flood waves due to their retention of flooding water (Anderson, Walling & Bates 1996; Grygoruk et al. 2013). At the same time, floodplains take up and transform nutrients and therefore play an important role in nutrient retention and cycling (e.g. Lautenbach et al. 2012; Natho et al. 2013). Floodplains also sequester a significant amount of carbon in the soil (Cierjacks et al. 2010) or in floodplain forests (Rieger et al. 2013). Further, floodplains provide diverse habitats for numerous species of plants, birds, amphibians, insects and other invertebrates (Naiman & Décamps 1997; Pollock, Naiman & Hanley 1998; Ward, Tockner & Schiemer 1999). Due to their high productivity, floodplains also provide food for these animal groups, as well as food and drinking water for humans (e.g. Lautenbach et al. 2012).

In Central Europe, the hydrologic conditions of most rivers have been heavily modified over recent centuries. For example, along the Elbe River, people began to build dikes approximately 800 years ago, which divided the floodplain into an active (directly inundated by river water at high water levels, also termed functional) and inactive (no longer directly inundated, also termed fossil) part (Leyer 2004). While the active floodplain is more or less regularly flooded directly with river water during high water levels, submergence in the inactive floodplain occurs indirectly through ascending ground water corresponding to the water level of the river.

Anthropogenic land use is a fundamental factor affecting floodplain vegetation along European rivers (Franke 2003; Krause *et al.* 2011). Without human impacts, functional floodplains in the European lowlands would be dominated by softwood (with *Salix* and *Populus* species) and hardwood (with *Ulmus* and *Quercus* species) floodplain forests (Dziock *et al.* 2005). The most abundant land use in the active floodplains of Central European lowlands is grazing and mowing. In these floodplain grasslands, species-rich vegetation developed, with a characteristic zonation of plant species from lower to higher elevated areas (Leyer 2002). These distinct zones of plant communities are thought to result from the soil moisture gradient from low to high elevations and from species-specific responses to annually varying groundwater levels (groundwater amplitude; Leyer 2002; Leyer 2005). Further, the zones of plant communities in floodplain grasslands are determined by seed and germination traits (Leyer & Pross 2009) and by competition (e.g. Jung *et al.* 2009). Due to the tightly intermingled vegetation zones, species density in floodplain grasslands is high (Donath, Hölzel & Otte 2003; Toogood, Joyce & Waite 2008). This kind of species-rich vegetation depends on low-intensity, but regular land use. Mowing once or twice annually (depending on the productivity of the site) without fertilizer application is recommended for facilitating a high species richness (Seffer, Janák & Sefferová Stanová 2008).

Species-rich floodplain meadows have declined strongly over the last centuries due to habitat losses mainly caused by land use changes (e.g. Wesche *et al.* 2012), river regulations (e.g. Tockner *et al.* 2002), and river training (Brunotte *et al.* 2009). Today, many species typical of floodplain grasslands are listed as rare and endangered for Germany (Ludwig & Schnittler 1996). Especially when the distribution of plant species is closely bound to floodplain ecosystems, such species seldom colonize alternative habitats outside of river corridors, which is the case with the so-called river corridor plants (Burkart 2001). Consequently, these meadows are of high conservation value and protected by the European Habitats Directive (92/43/EEC, habitat type 6440: Alluvial meadows of river valleys of the *Cnidion dubii*) and subject to various restoration measures (Jensen *et al.* 2006; Donath *et al.* 2007; Schmiede, Otte & Donath 2012). Nevertheless, remnants of species-rich floodplain meadows can be found today along many Central European rivers, such as the Elbe (e.g. Leyer 2002), Oder (e.g. Korsch 1999), Danube (e.g. Ružičková, Banásová & Kalivoda 2004), and Rhine (e.g. Hölzel & Otte 2001; Donath *et al.* 2003).

Climate change and its possible effects

Climate is an important driver determining plant distribution ranges (Woodward 1987). Thus, climatic changes will have large effects on the future distribution of plant species. Together with land use changes and increased nitrogen deposition, it is thought that climate change will be a serious threat for plant species diversity by the year 2100 (Sala *et al.* 2000).

Regional climate change projections indicate higher temperatures and an increasing risk of summer droughts for the late 21st century, due to less summer precipitation in western and northern Germany, in relation to the reference period 1961-1990 (Jacob *et al.* 2008; Görgen *et al.* 2010; Rechid 2014). Accordingly, reduced river discharges during summers are projected for the large rivers Rhine (Görgen *et al.* 2010) and Elbe (Conradt *et al.* 2012). In the adjacent floodplains, this could lower the groundwater table and the soil water potential. In combination with increased transpiration at higher temperatures, these changes could induce drought-stress in plants of floodplain meadows (Jensen *et al.* 2011).

Adapt or disperse – species under changing conditions have limited options to respond. One way plant species might react to climate change would be long-distance migration by dispersal to new sites that are climatically better suited for growth and reproduction. Already today, shifts in species ranges can be detected, which are interpreted as plant responses to climate change (Parmesan 2006). There is evidence, however, that many plant species are not able to migrate fast enough to new potential habitats (Honnay *et al.* 2002; Higgins *et al.* 2003; Bertrand *et al.* 2011; Zhu, Woodall & Clark 2012; Cunze, Heydel & Tackenberg 2013). In particular for rare and endangered species with small population sizes, successful migration through the highly fragmented landscape of Europe seems to be rather unlikely (Donath *et al.* 2003). Thus, the other option for persistence in a changing environment would be adaptation (Berg *et al.* 2010). In general, the adaptation potential of a plant species is affected by genetic variation and by phenotypic plasticity (Pauls *et al.* 2013). It still remains an open question as to how many plant species will be able to adapt to the relatively fast-changing conditions (Visser 2008). Niche-based models (including information on climate, soil, and land use) project negative impacts of climate change on species-richness in Germany for the period 2051-2080 (Pompe *et al.* 2008).

Survival and persistence of plant populations strongly depend on reproduction, thus seed germination and seedling establishment are the most critical stages in the life of plant individuals (Grubb 1977; Kitajima & Fenner 2000). Without successful germination and establishment, populations are threatened by extinction. Germination processes are affected by the biotic environment e.g. by competition from the established vegetation (Bakker & de Vries 1992; Kitajima & Fenner 2000), or by a litter layer (e.g. Jensen & Gutekunst 2003; Loydi *et al.* 2013), and by abiotic environmental conditions. In case of the latter, temperature and water availability are the main abiotic drivers of germination processes (Baskin & Baskin 2001; Fenner & Thompson 2005). Many species require specific environmental conditions for the germination process, and these factors are decisive for the subsequent seedling establishment (Baskin & Baskin 2001). As temperature and water availability are important drivers for the germination process, the changes induced by climate change will very likely affect this early stage in plant life (Walck *et al.* 2011). Consequently, species abundance and population dynamics might be altered, leading to distribution shifts or extinctions (Thuiller *et al.* 2005).

The impact of climate change on vegetation has received increasing attention recently. Different experimental approaches have already been conducted, focusing on CO_2 (e.g. Edwards, Clark & Newton 2001; Rasse, Peresta & Drake 2005), temperature (e.g. Klanderud & Totland 2005; Hudson, Henry & Cornwell 2011; Baldwin, Jensen & Schönfeldt 2014) or precipitation (e.g. Yahdjian & Sala 2002; Beier *et al.* 2012), and their effects on single species or plant communities. Some precipitation experiments have already been conducted in grassland ecosystems, e.g. in semi-arid steppe (Yahdjian, Sala & Austin 2006), in mesic tallgrass prairie (Fay *et al.* 2000), and in temperate grasslands (Grime *et al.* 2000; Bloor *et al.* 2010; Bütof *et al.* 2012; Walter *et al.* 2012). None of these studies focused on floodplain ecosystems. Further, modeling approaches have been used, which aimed at estimating climate-change-induced future species distributions and vegetation patterns (Pompe *et al.* 2008; Catford *et al.* 2013; Rivaes *et al.* 2013). Two of these studies addressed the combination of potential climate change effects and floodplains, but the focus was on Australian (Catford *et al.* 2013) and Mediterranean (Rivaes *et al.* 2013) floodplains. Overall, it is still largely unknown, how climate change will affect floodplain ecosystems.

Relevant questions concerning the effects of climate change on floodplain meadows

Is the influence of climate on floodplain meadows detectable under today´s climatic conditions?

While climate is usually considered to be an important driver determining plant distribution (see above), riparian vegetation, however, shows a so-called 'azonal' distribution, suggesting that this type of vegetation is not primarily influenced by climatic variables (Ellenberg & Leuschner 2010). Instead, other factors such as hydrologic conditions and land use are predominantly important for the vegetation of floodplains. Therefore, most studies on floodplain vegetation have mainly focused on the effects of such factors (e.g. Leyer 2004; Krause *et al.* 2011). The impact of regional climatic gradients on the composition and diversity of floodplain meadows is still unclear. If, however, climate affects the vegetation of floodplain meadows today, it might be assumed that climate change may lead to vegetation changes in the future. To estimate the effects of future climate change on the vegetation of floodplain meadows it is, therefore, essential to investigate the effects climate has today on this type of vegetation (chapter 2).

Are projected future climatic conditions suitable for the germination of floodplain meadows species?

To estimate future distribution and abundance of plant species, it is essential to gain knowledge of their specific requirements for seedling recruitment (e.g. Adler & HilleRisLambers 2008; Walck *et al.* 2011). While most of the above-mentioned approaches (page 4) for analyzing the effects of climate change on vegetation focused on mature plants, little work has been done considering the early life stages. Here, one possible approach is to investigate germination at different water availabilities, with seeds exposed to different water potentials (e.g. Fyfield & Gregory 1989; Swagel, Bernhard & Ellmore 1997; Akhalkatsi & Lösch 2001). To date, most studies in which water potentials were manipulated focused on germination traits of single plant species, whereas comparative studies on a larger number of species are scarce (but see Evans & Etherington 1990). Moreover, rare plant species and the influence of hydrological factors on their germination have only rarely been investigated (but see Geißler & Gzik 2008a) and only one study investigated whether germination differs between species indicative of different habitats (Evans & Etherington 1990). However, analyzing the responses of plant functional groups (based on key life-history traits) to climatic changes appears a promising approach (Ooi 2012) – an enterprise undertaken in the framework of this thesis (chapter 3).

Is the use of floodplain meadows` hay sustainable under future precipitation conditions?

A prerequisite for the sustainable conservation of floodplain grasslands is that they are continuously used, i.e. non-intensively but frequently cut or grazed. How the biomass of non-intensively managed meadows can be incorporated into agricultural land use systems is an ongoing nature conservation concern (Donath *et al.* 2004; Isselstein, Jeangros & Pavlu 2005). As it is preferable to integrate these meadows into farming systems rather than just to manage them in the framework of nature conservation schemes, the yield of low input species-rich grasslands has to be explored (Isselstein *et al.* 2005). Additionally, the future yield of semi-natural grasslands may be affected by decreased summer precipitation due to climate change. Only one of the above-mentioned climate change studies (page 4) focused on how the ecosystem service of forage quality might change in the future, using the example of nitrogen and protein content of the biomass (Walter *et al.* 2012). While data on the forage quality of non-intensively used semi-natural grasslands is generally scarce in the international literature (but see Donath *et al.* 2004; Klaus *et al.* 2011), the variables relevant for farmers, such as crude fibre, crude protein, energy content, or fructan, are almost completely lacking in this context. Therefore, I have addressed this topic as one objective of this thesis (chapter 4).

How will indirect effects of climate change influence the species of floodplain meadows?

Besides the direct effects of climate change, indirect effects on vegetation are also possible. As mentioned above (page 3), the altered climate might lead to reduced water levels in rivers, especially during summer. This could possibly lower the groundwater table in the adjacent floodplains. As the hydrologic conditions are the most important factor in floodplains, how plant species might respond to water level changes is of interest. Species usually have a specific physiological optimum in relation to the hydrological regime (Silvertown *et al.* 1999; van Eck *et al.* 2004). Under competition, however, some species shift their occurrence along hydrological gradients away from their physiological optimum to conditions where competition is lower (ecological optimum *sensu* Ellenberg 1954). Hence, the plant–plant interaction ‘competition’ is, another important factor shaping plant communities in floodplains (Ellenberg 1954; Grime 1979). Knowledge is scarce about the performance of plants at different water levels and in response to competition, especially for the rare and endangered plant species (such as the river corridor plants). If such knowledge existed, it would be possible to develop management strategies to support the plant species of conservation interest. In this thesis, therefore, the effects of water level and competition on plant performance were investigated for the endangered river corridor plant *Cnidium dubium* (chapter 5).

The projects KLIMZUG-Nord and KLIWAS

The studies were conducted in the framework of the projects KLIMZUG-Nord and KLIWAS. The vegetation study along the Elbe River (chapter 2), the two experiments carried out at tributaries of the Elbe (chapter 4) and the water level experiment with *Cnidium dubium* (chapter 5) were part of the project KLIMZUG-Nord (2009-2014), which aimed at developing adaptation strategies for climate change in the metropolitan region of Hamburg. The experiments at the Rhine River (chapter 4) and the germination experiment (chapter 3) were part of KLIWAS (2010-2013), a project which aimed at evaluating the effects of climate change on German federal waterways and their floodplains. While the practical work of this thesis relating to KLIMZUG-Nord was conducted in the Applied Plant Ecology working group at the University of Hamburg (chapters 2, 4 and 5), the practical work as part of KLIWAS was conducted in the working group Landscape Ecology and Resource Management at the Justus-Liebig University of Giessen (chapters 3 and 4).

Study area: Floodplains at the Elbe and Rhine River

All studies of this thesis were conducted on or with species originating from floodplain meadows located in functional floodplains of the rivers Elbe and Rhine and of two Elbe River tributaries, the Havel and the Sude River. All studied floodplains have in common the fact that the climatic and hydrological conditions result in highly variable soil water potentials. While winter, spring and early summer often bring floods, the summer periods are notably dry (especially the continental sites at the eastern part of the Elbe gradient, the Havel site, and the Rhine site). Along with the strong seasonal and inter-annual fluctuation of the water level of the rivers, the groundwater tables also fluctuate strongly (Elbe: Leyer 2002; Rhein: Bissels et al. 2005).

Study sites along the Middle Elbe River

The studied floodplain meadows of the Elbe region are located in the UNESCO Biosphere Reserve Elbe River Landscape. In the study presented in chapter 2, six sites were selected in the functional floodplain along the regional climatic gradient of the Middle Elbe River (Fig. 1.1): 1 - Bleckede (53°20’ N, 10°43’ E; northern-most site), 2 - Strachau, 3 - Schnackenburg, 4 - Fischbeck, 5 - Steckby, and 6 - Wörlitz (51°51’ N, 12°26’ E; southern-most site). At these sites, two types of floodplain grasslands were investigated: wet and mesic meadows. The wet meadows were characterized by high abundances of *Phalaris arundinacea*, *Symphytum officinale*, and *Sium latifolium*. The mesic meadows were characterized by high abundances of *Alopecurus pratensis*, *Cnidium dubium*, and *Rumex thyrsiflorus*. The climate along these study sites is characterized by relatively continental conditions in the south-east and oceanic conditions in the north-west. The area in the north-west receives approx. 20 % higher mean annual precipitation than the area in the south-east, while *vice versa* the area in the south-east has approx. 25% more summer days (days > 25°C).

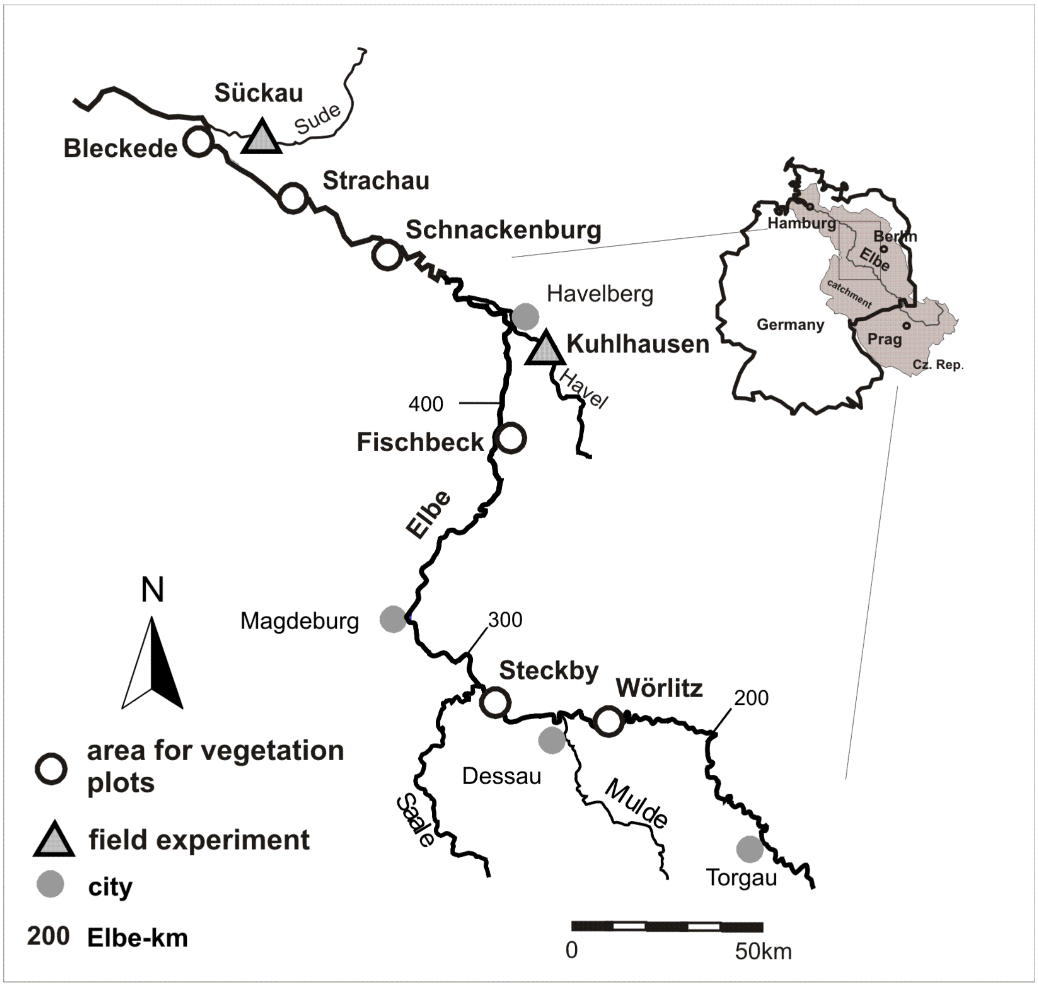

Fig. 1.1: Map with the study sites along the Elbe River. In the functional floodplain of the Elbe River, the plots are located for the vegetation survey described in chapter 2 (marked with circles). The field experiments described in chapter 4 (marked with triangles) were located in the functional floodplains of the Sude and Havel Rivers (Cartography by Mathias Scholz).

The meadows investigated in chapter 4 are located at Elbe tributaries at the Havel River (near Kuhlhausen in Saxony-Anhalt, N52°46' E12°12') and the Sude River (near Sückau in Lower Saxony, N53°19' E10°57'), and represent contrasting positions along the above-mentioned climatic gradient. The north-western site at the Sude River experiences rather oceanic conditions, with a mean annual precipitation of 663 mm and a mean annual temperature of 8.3°C (1961-1990; data from the nearest weather station in Boizenburg; DWD 2013). The south-eastern site at the Havel River has, by way of contrast, relatively continental conditions, with a mean annual precipitation of 503 mm (1961-1990; data from the nearest weather station in Havelberg; DWD 2013) and a mean annual temperature of 9.1°C (1976-2009; data from the nearest weather station measuring temperature in

Seehausen; DWD 2013). They are regularly flooded by either the Sude or the Havel River, which are first order tributaries of the Elbe River.

The soils of both sites are gleyic Fluvisols which consist mainly of loamy material over sandy sediments. The active floodplains along the Sude and Havel are typically used as grasslands, and the two meadows are mowed twice annually. Both study sites contain floodplain meadow vegetation with characteristic river corridor plants, such as *Cnidium dubium, Stellaria palustris* and *Carex vulpina*, and more frequently occurring species, such as *Alopecurus pratensis*, *Deschampsia cespitosa*, *Potentilla anserina*, *Potentilla reptans*, and *Ranunculus repens*.

Study site at the Upper Rhine River

The study area at the Rhine River is situated in the Hessian part of the Holocene floodplain of the northern Upper River Rhine near Riedstadt, about 30 km southwest of Frankfurt, Germany (N 49°49', E 8°26'). The climate in this area is relatively dry and warm, with a mean annual precipitation of 602 mm (1961-1990 Riedstadt-Erfelden, DWD 2013) and a mean annual temperature of 9.7°C (1961-1990 Frankfurt Main airport, DWD 2013). The soils can be classified as calcic Fluvisols (Burmeier et al. 2010). The vegetation of the study site itself is relatively species-poor because it was an arable field before 1983 (for details on the history of the site see Böger 1991, Bissels et al. 2004). Since 1983, the meadows have been mown up to two times annually. Two areas differing in elevation above the base flow were chosen as study sites (a higher/dryer site and a lower/wetter site). The species composition of the studied meadow is dominated by *Festuca arundinacea*. Further frequently occurring species are *Dactylis glomerata* and *Leucanthemum vulgare* on the higher elevated site, and *Potentilla reptans* and *Symphytum officinale* on the lower elevated site.

Objectives and chapter outline

The overall aim of this thesis was to elucidate possible effects of climate change on Central European floodplain meadows. Therefore, four research objectives were addressed. In the first step, it was analyzed if an influence of regional variation in climate on the vegetation of floodplain meadows along the Middle Elbe River is detectable under current climatic conditions. In the following steps, the effects of changing climatic and/or environmental conditions on the vegetation or selected species of floodplain meadows were investigated on multiple scales in climate chamber, common garden and field experiments.

Chapter 2: Vegetation patterns of floodplain meadows along the climatic gradient at the Middle Elbe River

The vegetation of two types of floodplain meadows was studied along the regional climatic gradient of the Middle Elbe River. This gradient exhibits rather continental conditions in the south-east and oceanic conditions in the north-west. The study aimed at detecting the influence of current climate on the vegetation of floodplain meadows along this gradient.

Research questions: 1) How does the composition and diversity of the vegetation of floodplain meadows change along the Middle Elbe River? 2) If changes occur, are these correlated with climatic variables? 3) Does the proportion of plant species with a rather continental distribution increase in the eastern part of the studied gradient along the Elbe River (as an indication for the climatic influence)? 4) How are typical floodplain meadow species (river corridor plants) distributed along the Middle Elbe River?

Ludewig, K., Korell, L., Löffler, F., Scholz, M., Mosner, E. & Jensen, K. (2014): Vegetation patterns of floodplain meadows along the climatic gradient at the Middle Elbe River. *Flora*, 209, 446-455. DOI: 10.1016/j.flora.2014.04.006

Chapter 3: Differential effects of reduced water potentials on the germination of floodplain grassland species indicative of wet and dry habitats

The seeds of 20 floodplain meadow species with different moisture requirements from five plant families were exposed to a water potential gradient (ranging from 0 to -1.5 MPa) and to two temperature regimes (15/5 °C and 20/10 °C). Additionally, seeds of five species were collected at the Elbe and at the Rhine River, in order to compare the germination characteristics of seeds from two origins.

Research questions: 1) Do reduced water potentials affect the germination patterns of all plant species? 2) Does the temperature regime affect germination? 3) Do seeds originating from populations at the Elbe differ in their response to reduced water potentials, compared to those from populations along the Rhine? 4) Does seed germination of floodplain plant species indicative of wet habitats differ to those floodplain plant species indicative of dry habitats?

Ludewig, K., Zelle, B., Eckstein, R.L., Mosner, E., Otte, A. & Donath, T.W. (2014) Differential effects of reduced water potentials on the germination of floodplain grassland species indicative of wet and dry habitats. *Seed Science Research*, 24, 49-61. DOI:10.1017/S096025851300038X

Chapter 4: Effects of reduced summer precipitation on forage quantity and quality of floodplain meadows at the Elbe and Rhine River

Effects of reduced summer precipitation on the quality of the harvested hay were investigated in field experiments on floodplain meadows at two Elbe tributaries (from 2009-2011) and at the Rhine River (2011-2013). We reduced summer precipitation using rainout shelters and additionally simulated N-deposition at the Elbe River. As response variables, we measured the amount of hay biomass, its contents of crude protein, crude fibre, energy, fructan, nitrogen, phosphorus, and potassium.

Research questions: Does reduced summer precipitation affect 1) the productivity, 2) the quality of hay, and 3) the overall energy yield of floodplain meadows?

Ludewig, K., Donath, T.W., Zelle, B., Eckstein, R.L., Mosner, E., Horchler, P., Otte, A. & Jensen, K. (submitted) Effects of reduced summer precipitation on forage quantity and quality of floodplain meadows at the Elbe and Rhine River, *PLOS One*.

Chapter 5: Effects of water level and competition on the endangered river corridor plant Cnidium dubium *in the context of climate change*

The response of *Cnidium dubium* to differing water levels was investigated in mesocosm experiments. The plants originated from two floodplain meadows at tributaries of the Elbe River. In one experiment, we investigated growth characteristics and biomass of juvenile *Cnidium dubium* individuals in response to water level (20, 40, and 60 cm below soil surface). The juvenile plants were raised from seeds collected at the two tributaries Havel and Sude River. In a second experiment, competitors were included to analyze interactive effects of competition and water level on mature plants of *Cnidium dubium*. The mature plants were sampled in sods at the two tributaries, Havel and Sude River.

Research questions: 1) At which water level does *Cnidium dubium* perform best without competing plants? 2) How do the different water levels influence the growth of *Cnidium dubium* under competition? 3) Do the juveniles grown from seeds of different origins differ in their growth in response to the applied water levels?

Hanke, J.M., Ludewig, K. & Jensen, K. (2014) Effects of water level on the endangered river corridor plant *Cnidium dubium* with and without competition. *Wetlands, Ecology and Management,* published online 12.8.2014. DOI: 10.1007/s11273-014-9371-5

Chapter 6: Possible effects of climate change on the vegetation of floodplain meadows – Synthesis

In this section, the main results and conclusions are discussed in the context of the published literature and with regard to management options to mitigate possible negative impacts of climate change.

For consistency throughout this thesis, the figures and tables of all manuscripts were renumbered and all references were summarized at the end of the thesis. Further, a missing sigma sign was added to the formula in chapter 3 (page 42).

CHAPTER 2

VEGETATION PATTERNS OF FLOODPLAIN MEADOWS ALONG THE CLIMATIC GRADIENT AT THE MIDDLE ELBE RIVER

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Abstract

Central European floodplain meadows are characterised by flooding mainly in winter/spring and dry conditions over the summer. They harbour many rare and endangered plant species. We studied the vegetation of floodplain meadows along the regional climatic gradient of the Middle Elbe River. This gradient exhibits rather continental conditions in the south-east and oceanic conditions in the north-west. We aimed at detecting the influence of climate on the vegetation of floodplain meadows along this gradient.

Along the Middle Elbe River (Germany), we recorded the vegetation of wet and mesic meadows in 2010. The results revealed differences in species composition especially in wet meadows: Vegetation plots of wet meadows clustered in the DCA-ordination according to their geographic location from west to east. Sample scores of DCA-axes of both meadow types correlated with the long-term means of climatic factors such as precipitation or temperature. While species numbers did not differ between study sites, evenness of mesic meadows was higher in the western part of the gradient.

Indicative species of the sites were mainly common meadow species. Species typical for floodplain meadows were relatively evenly distributed along the gradient. Therefore, we confirm that the distribution of typical floodplain species is largely determined by hydrologic and land use conditions rather than by climatic factors. Therefore, we assume that typical floodplain meadow species at the Elbe River are relatively robust against direct climatic changes, as long as these changes do not exceed the range of the climatic gradient today. Concerning the total assemblages of floodplain meadows, those of wet meadows might be more vulnerable to climate change than those of mesic meadows. However, indirectly occurring changes caused by climate change, i.e. water-level changes due to an altered discharge regime of the Elbe River caused by altered precipitation patterns in the catchment, will affect all floodplain species.

Keywords

Azonal vegetation * alluvial meadows * climatic impact * riparian meadows * river corridor plants

Introduction

Floodplain meadows belong to the most threatened plant communities in Europe (Korneck et al. 1996; Joyce and Wade 1998). The hydrologic conditions of most Central European rivers were heavily modified over the recent centuries. For example along the Elbe River, people began to build dikes approximately 800 years ago, which divided the floodplain into a functional floodplain (directly inundated by river water at high water levels) and a fossil (no longer directly inundated) floodplain (Leyer 2004). Additionally, land use intensification and abandonment caused a dramatic decline of species rich floodplain meadows since the middle of the 20th century (Leyer 2002; Krause et al. 2011). Due to this decline and the large number of rare and endangered plant species, floodplain meadows are protected by the EU Habitats Directive (92/43/ECC; habitat type 6440: alluvial meadows of Cnidion dubii). Still, floodplain meadows can be found today along many Central European rivers such as the Elbe (e.g. Leyer 2002), Oder (e.g. Korsch 1999), Danube (e.g. Ružičková et al. 2004), and Rhine (e.g. Donath et al. 2003; Hölzel and Otte 2001).

Climate is considered to be an important driver determining plant distribution ranges on a global scale (e.g. Woodward 1987). Riparian vegetation, however, generally shows a so called 'azonal' distribution, suggesting that this type of vegetation is not primarily influenced by climatic variables (Ellenberg 1996). Instead, other factors such as hydrologic conditions and land use are predominantly important for the vegetation of floodplains (e.g. Leyer 2004; Krause et al. 2011).

Previous studies on floodplain vegetation mainly focused on the effects of hydrologic conditions as the most important factor affecting functional floodplains, especially the aspect of flooding (e.g. Leyer 2004; Follner and Henle 2006; Marchetti and Aceñolaza 2013). Flooding usually causes erosion and sedimentation (Krüger et al. 2006), temporarily anaerobic soil conditions (Langer and Rinklebe 2009), and affects the nutrient regime of the soils (Beltman et al. 2007). Flooding supports species which are adapted to it (Blom and Voesenek 1996). In floodplain areas at higher elevations, which mainly consist of sandy sediments, drought stress gains importance during summer.

Land use is another important factor affecting floodplain vegetation (Franke 2003; Krause et al. 2011). Without human impacts, functional floodplains in the European lowlands would be dominated by softwood (with *Salix* and *Populus* species) and hardwood (with *Ulmus* and *Quercus* species) floodplain forests (Dziock et al. 2005). The most abundant land use in the functional floodplains of Central European lowlands is grazing and mowing. Especially in mown grasslands (floodplain meadows), species-rich vegetation with a characteristic zonation of plant species from lower to higher elevated areas developed (Leyer 2002). This kind of vegetation depends on low-intensity but regular land use (i.e. mowing twice annually without applying fertilizers).

The impact of regional climatic gradients on the composition and diversity of floodplain meadows is still unclear. If, however, the climate affects the vegetation of floodplain meadows today, climate change may lead to vegetation changes in the future. Our overall aim was thus to assess, how vulnerable the vegetation of floodplain meadows might be to climate change. Our study area, the Middle Elbe region, is suitable for addressing this topic as the climatic differences along this part of the river are pronounced although the geographic range is relatively short (app. 250 km). The observed response patterns, though based on a study along the Elbe River, might be applicable to other floodplain regions such as along the rivers Oder, Danube or Rhine, which also cover quite a range of different climatic conditions.

We conducted a field survey and investigated two floodplain meadow types differing in hydrologic conditions: wet (more frequently flooded) and mesic (less frequently flooded) meadows. Other factors as land use and soil conditions were sought to be as equal as possible. We addressed the following research questions: 1) How does the composition and the diversity of vegetation of floodplain meadows change along the Middle Elbe River? 2) If changes occur, are these correlated with climatic variables? 3) Does a higher proportion of plant species with a rather continental distribution grow in the eastern part of the studied gradient along the Elbe River (as an indication for the climatic influence)? 4) How are typical floodplain meadow species (river corridor plants) distributed along the Middle Elbe River?

Material & Methods

Study area

The study was conducted on floodplain meadows of the UNESCO Biosphere Reserve Elbe River Landscape (Fig. 2.1). The Elbe River is one of the largest rivers in Central Europe and flows about 1,100 km from the Czech Giant Mountains through the lowlands of Germany to the North Sea. The Elbe is divided into three parts (the Upper, Middle and Lower Elbe) and drains a discharge area of approx. 150,000 km² (for detailed information see Hofmann et al. 2005). For this study, only locations along the middle part of the Elbe River were selected to ensure a comparable morphology of the study sites (regarding ground slope and grain size of sediments). The morphology of this river corridor was created during the last ice ages while the river served as a glacial valley. The discharge during the ice ages and following ice melts was much higher than today and thus an extended river corridor was formed. The climate of the study area is characterised by relatively continental conditions in the south-east and oceanic conditions in the north-west (Table 2.1). The area in the north-west receives approx. 20% more mean annual precipitation than the area in the south-east, while *vice versa* the area in the south-east has approx. 25% more summer days (days > 25°C). The semi-terrestrial soils of the Elbe floodplains consist mainly of loamy material. Other alluvial sediments such as sand and gravel are present but of minor importance (Schwartz 2001). Nutrient availability of these soils is high due to nutrient inputs from flooding events. Generally, flooding of the Elbe occurs regularly during winter and spring after snow melt and infrequently during summer after intense rain events. Flooding events are mainly restricted to the functional floodplain (Leyer 2004), which decreased in extent by around 50-90% over the last hundreds of years along the Middle Elbe River (Brunotte et al. 2009). The functional floodplain along the Elbe River is mainly used as grassland for grazing and mowing. In Lower Saxony, for example, these two land use types are equally important (Franke 2003). For this study, only meadows were selected that are usually mown twice annually without the application of fertilizers (pers. comm. with local farmers).

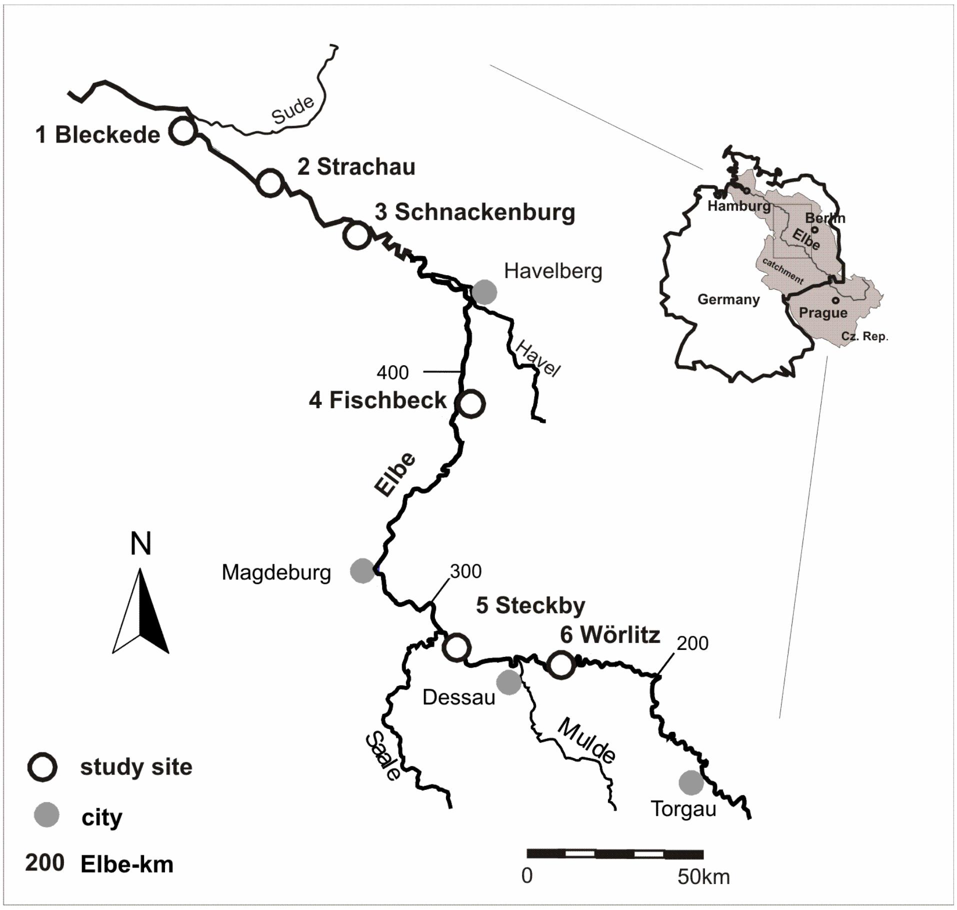

Fig. 2.1: Study area with study sites along the gradient at the Middle Elbe River; numbered from north-west to south-east: 1 — Bleckede, 2 — Strachau, 3 — Schnackenburg, 4 — Fischbeck, 5 — Steckby, and 6 — Wörlitz.

Study sites and sampling

Six sites were selected in the functional floodplain along the Middle Elbe River (Fig. 2.1): 1 — Bleckede (53°20’ N, 10°43’ E; northern most site of the gradient), 2 — Strachau, 3 — Schnackenburg, 4 — Fischbeck, 5 — Steckby, and 6 — Wörlitz (51°51’ N, 12°26’ E; southern most site of the gradient). At these sites, vegetation was recorded on overall 46 plots (each measuring 25 m^2) on two types of floodplain meadows:

a) Wet meadows characterised by high abundances of *Phalaris arundinacea*, *Symphytum officinale*, and *Sium latifolium* (Bleckede: 4 plots, Strachau: 4, Schnackenburg: 5, Fischbeck: 4, and Steckby: 3). In Wörlitz no plots were sampled on wet meadows for logistical reasons.

b) Mesic meadows characterised by high abundances of *Alopecurus pratensis*, *Cnidium dubium*, and *Rumex thyrsiflorus* (Bleckede: 4 plots, Strachau: 5, Schnackenburg: 4, Fischbeck: 4, Steckby: 4, and Wörlitz: 5).

The plots were randomly distributed on the meadows based on habitat maps (random points were calculated using ArcGIS software, Esri Inc. CA/USA, following Henle et al. 2006). In May and June 2010 plant species abundance was recorded on all plots according to the Braun-Blanquet cover-abundance scale (Braun-Blanquet 1964) and then transformed into percentage values (r = 0.01%, + = 0.2%, 1 = 2.5%, 2 = 15%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%). The nomenclature of plant species follows Wisskirchen & Haeupler (1998).

Table 2.1: Climatic parameters of the six study sites: Temperature 7100 = mean annual temperature (1971-2000), Precipitation 7100 = mean annual precipitation (1971-2000), Summer days 7108 = mean annual number of days > 25°C (1971-2008), Frost days 7109 = mean annual number of days < 0°C (1971-2009)

Position along gradient Site Elbe-River-km	1 Bleckede 553-554	2 Strachau 520-522	3 Schnackenburg 473-474	4 Fischbeck 387-388	5 Steckby 283-285	6 Wörlitz 242-243
Temperature 7100 (°C)	8.9	9.0	9.0	9.2	9.5	9.5
Precipitation 7100 (mm a^{-1})	635	601	560	509	498	544
Summer days 7108 (no. of days>25°C a^{-1})	30	33	36	41	41	43
Frost days 7109 (no. of days<0°C a^{-1})	67	71	78	78	73	75

Environmental variables

Climate data were provided by Germany's National Meteorological Service (DWD) as a digital map with spatially interpolated values of climate variables. The values of the climatic variables were attributed to the coordinates of the study plots using ArcGIS software (Esri Inc. CA/USA).

The elevation of the study plots (NN) was measured using a differential GPS 'Trimble 5700' except for Bleckede and Schnackenburg for which we used the digital ground model DGM-W Elbe Nord provided by the Lower Saxony Water Management, Coastal Defence and Nature Conservation Agency (NLWKN). Based on the elevation, the mean flooding duration of each plot was calculated for a period of five years (2005-2009). Therefore, daily time series of water level values from the nearest water level gauges of each location were gained from the authorities WSA Lauenburg (gauges Hitzacker and Bleckede), WSA Magdeburg (gauges Tangermünde and Schnackenburg) and WSA Dresden (gauges Coswig and Aken). Because of the ground slope, we corrected differences between the elevation of the study locations and the gauges on the basis of the differences in mean water levels calculated by a one-dimensional hydrodynamic-numerical model (data provided by BfG, Germany). Flooding duration was estimated by summing up the days with water levels higher than the elevation of the study plots. This was done for each year (2005-2009) and averaged to a mean flooding duration (in days per year) for all plots. For two study plots at the location Steckby, we calculated the flooding duration according to Follner and Henle (2006), because our first method underestimated the flooding duration of these two plots as the Elbe tributary Funder is primarily affecting these sites.

Statistical analysis

As a measure of diversity we calculated species number (S) and Buzas and Gibson's evenness (e^H/S where e is the natural logarithm and H is the value of the Shannon index) for each vegetation plot using PAST (Hammer et al. 2001). To analyse the abundance of river corridor plants, we summed up the percentage abundance of all river corridor plant species (based on Burkart 2001) per plot. Differences in species numbers, Buzas and Gibson's evenness and abundance of river corridor plants between locations along the gradient were analysed with one-way ANOVAs, separately for both habitat types (due to the unbalanced sampling design). ANOVAs with significant results were followed by Tukey HSD-tests. Basic requirements to conduct a parametric ANOVA such as normality and homoscedasticity were visually checked using diagnostic plots.

Detrended correspondence analysis (DCA) was used to reveal vegetation patterns along the climate gradient of the Elbe River. Plant species that were recorded in the data sets (all meadows, wet meadows, and mesic meadows) less than three times were excluded to reduce the disproportional influence of rare species in these analyses. Finally, 83 plant species were included in the ordination of the complete data set (46 plots), 44 plant species were included in the ordination of wet meadows (20 plots) and 58 species in the ordination of mesic meadows (26 plots). For the analyses of wet and mesic meadows, sample scores of the first three DCA axes were correlated with environmental variables using Pearson’s correlation. Additionally, indicator value analyses (IndVAL-analyses) were performed separately with all species for both meadow types following Dufrene & Legendre (1997) to determine characteristic species for each site. This analysis takes the abundance and frequency of species into account, provides an indication value ranging from 0 (no indication) to 1 (perfect indication), and calculates a significance value for each species.

Further, we analysed whether species with a rather continental distribution occur more frequently in the eastern part of the gradient and *vice versa* for species with a rather oceanic distribution. Information about the distribution ranges of species was taken from the BiolFlor database (Kühn et al. 2004). In BiolFlor the distribution range of species is classified into eight classes (eu-oceanic, slightly oceanic, sub-oceanic, slightly sub-oceanic, slightly sub-continental, sub-continental, slightly continental, eu-continental). A continentality class could be assigned to 103 of the 118 species in our data set (see Appendix 1). We pooled all classes that were “oceanic” and all classes that were “continental”, and additionally pooled the sites 1 – 3 (Bleckede, Strachau and Schnackenburg) as “western” and 4 – 6 (Fischbeck, Steckby and Wörlitz) as “eastern” sites to minimize the influence of the single location. We used t-tests to analyse whether the frequency of rather oceanic and rather continental species differs between western and eastern study sites.

IndVAL-Analyses were performed using the labdsv package of David W. Roberts in R (R Development Core Team 2008), univariate analyses were processed using STATISTICA 9 (StatSoft 2009) and multivariate analyses were performed using PC-ORD (McCune and Mefford 2006).

Results

Species richness, evenness and vegetation patterns of both meadow types

118 vascular plant species were recorded on the 46 vegetation plots. 13 of these species could be classified as river corridor species (Burkart 2001). Species number did not differ between sites in either of the meadow types (Wet: $F_{4,15} = 2.1$, $p = 0.13$; Mesic: $F_{5,20} = 1.8$, $p = 0.17$; Fig. 2.2a). Buzas and Gibson's evenness differed between sampling sites in both meadow types (Wet: $F_{4,15} = 3.4$, $p = 0.04$; Mesic: $F_{5,20} = 10.0$, $p < 0.0001$; Fig. 2.2b). While in mesic meadows the evenness was higher in sites one and three (Bleckede and Schnackenburg) compared to sites four, five and six (Fischbeck, Steckby and Wörlitz; Fig. 2.2b), the post-hoc test revealed no significant differences between sites of wet meadows, although the factor site was significant in the ANOVA. The DCA including both meadow types revealed that the species composition of wet meadows differed from those of mesic meadows as the plots of both meadow types clustered separately from each other along the second DCA axis (gradient length of the second DCA axis: 3.2; total inertia: 5.1; Fig. 2.3). While the factor flooding duration corresponded with axis 2 along which the two meadow types were separated, the precipitation in summer and spring corresponded with axis 1 (gradient length of first axis: 3.0).

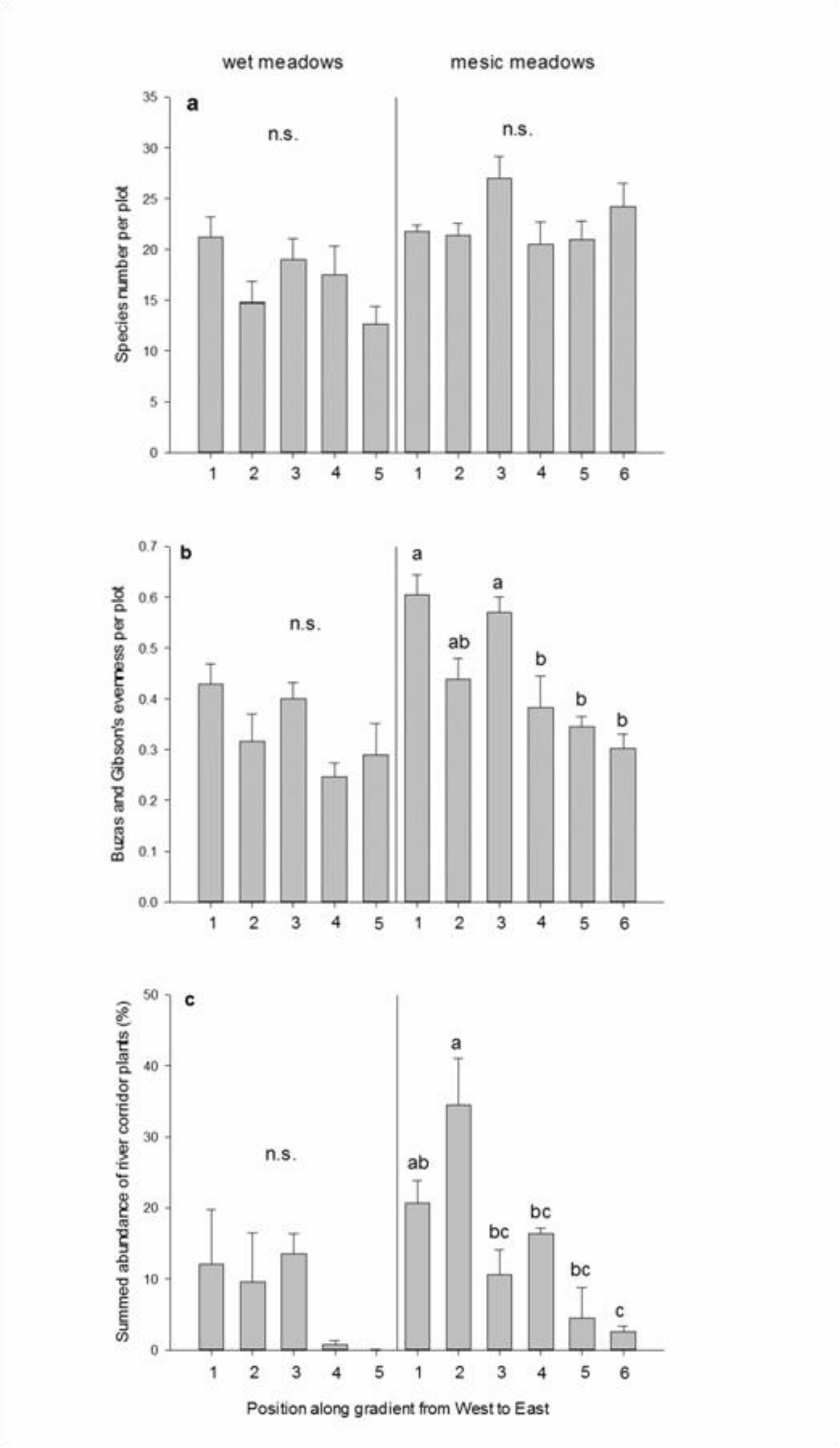

Fig 2.2: Species number (a), Buzas and Gibson´s evenness (b), and summed abundances (%) of river corridor plants (c) per plot according to meadow type and site (means + SE). Significant differences between sites are indicated by different letters. n.s. = no significant differences. For locations of sites (1 — Bleckede, 2 — Strachau, 3 — Schnackenburg, 4 — Fischbeck, 5 — Steckby, and 6 — Wörlitz) see Fig. 2.1. At site six no wet meadows were sampled.

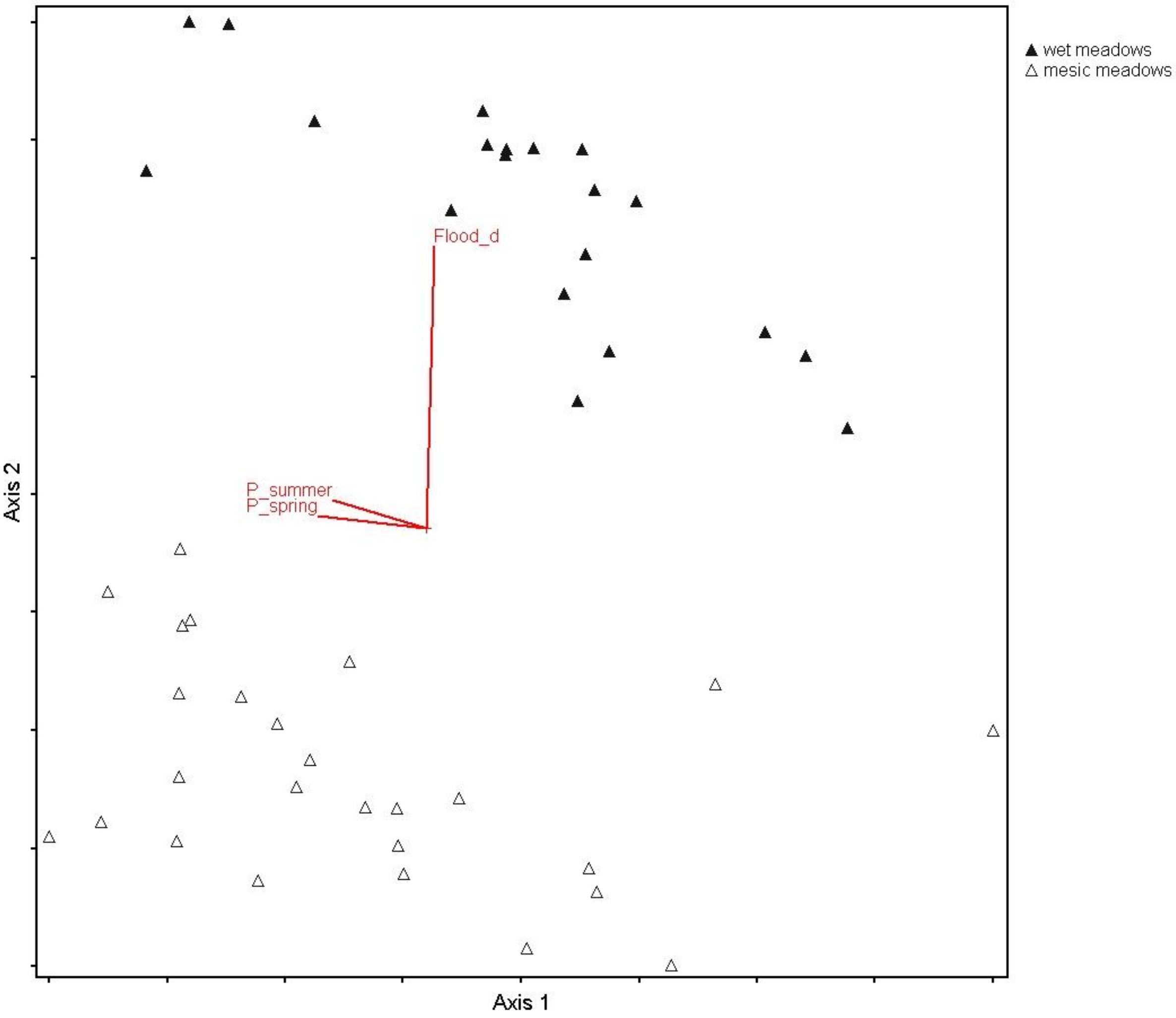

Fig. 2.3: DCA ordination of wet and mesic meadows based on the abundance of 83 plant species of 46 vegetation plots; total inertia: 5.1; axis 1: eigenvalue 0.37, gradient length 3.0 SD, axis 2: eigenvalue 0.52, gradient length 3.2 SD. For abbreviations of environmental variables: see Table 2.2.

Wet meadows

Species composition of wet meadows changed along the Middle Elbe River (Fig. 2.4). The plots of the five sites were arranged along the first axis in the DCA ordination according to their geographic location along the West-East gradient (gradient length of first DCA axis: 2.7; total inertia: 2.2). Only the plots of Strachau were found near to those of Fischbeck and Schnackenburg in relation to the first axis. They were separated along the second axis. The first axis in the DCA was positively correlated with the mean long-term annual and seasonal temperature (except for winter temperature) and negatively correlated with long-term annual and seasonal precipitation. Mean temperature in winter was positively correlated with the second axis (see Table 2.2).

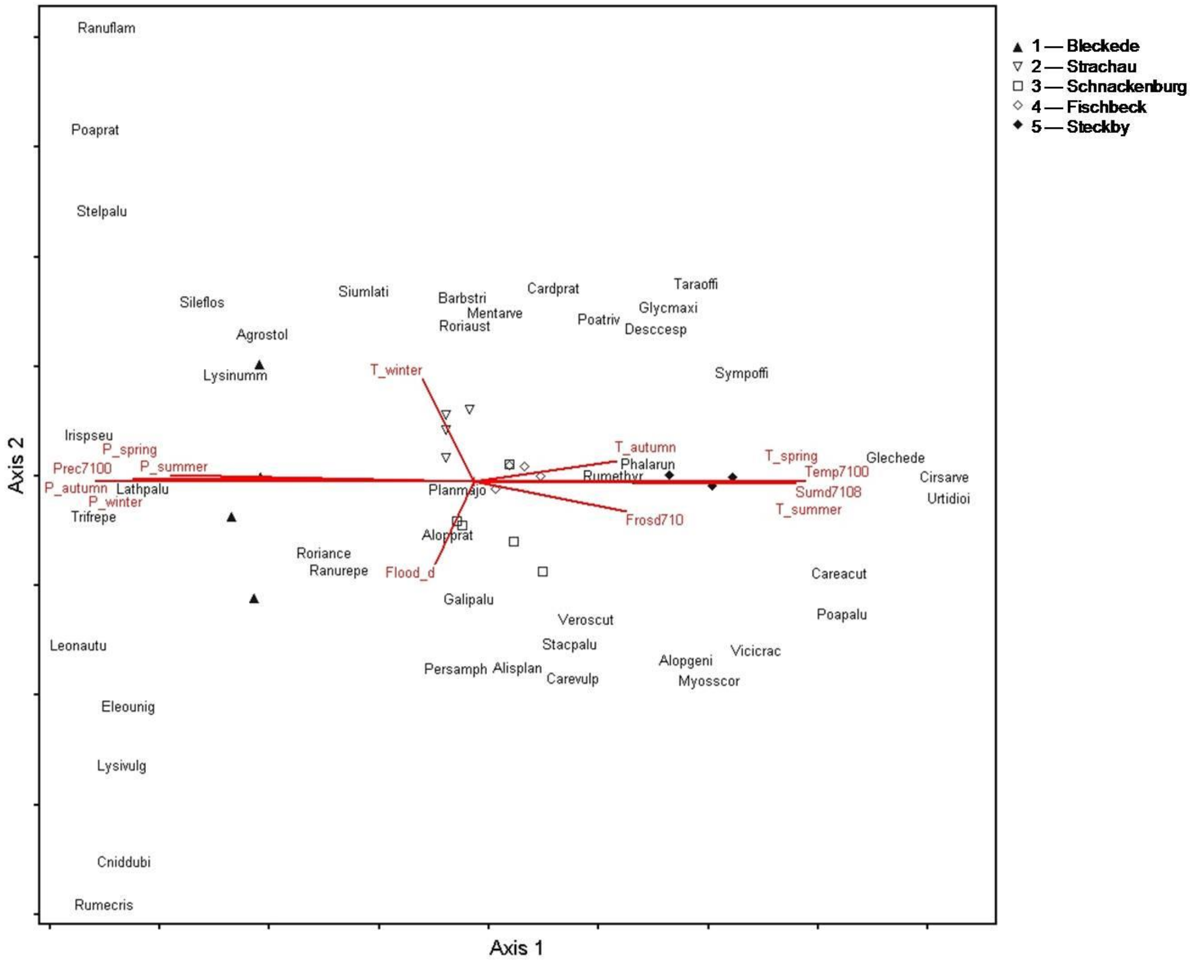

Fig. 2.4: DCA ordination tri-plot of the wet meadows based on the abundance of 44 plant species of 20 vegetation plots; total inertia: 2.2; axis 1: eigenvalue 0.45, gradient length 2.7 SD, axis 2: eigenvalue 0.21 gradient length 1.9 SD. For abbreviations of environmental variables: see Table 2. For acronyms of species: see Appendix 2.1.

Species affecting these vegetation patterns were plotted in the DCA ordination (Fig. 2.4) and additionally detected by the IndVAL-analysis (Table 2.3). Between three and six species were detected as characteristic for each study sites. Species characteristic for western most location 1 were e.g. *Leontodon autumnalis*, *Stellaria palustris*, *Trifolium repens*, or *Iris pseudacorus*, all distributed on the left side of the DCA ordination. Species characteristic for the eastern most location 6 were e.g. *Urtica dioica*, *Cirsium arvense* and *Glechoma hederacea*, which were also displayed on the right side of the DCA ordination. The patterns of the differentiated species composition of wet meadows along the Middle Elbe River (Fig. 2.4) were mainly determined by different abundances of common meadow species, as only few of the indicative species were river corridor plant species (Table 2.3).

Table 2.2: Correlation coefficients between wet meadow's DCA sample scores of the first three axes and environmental variables. Temperature 7100 = Mean annual temperature (1971-2000), Precipitation 7100 = mean annual precipitation (1971-2000), Summer days 7108 = mean annual number of days > 25°C (1971-2008), Frost days 7109 = mean annual number of days < 0°C (1971-2009), Flood days 0509 = mean annual number of days with water level above the height of site (2005-2009); spring: March-May, summer: June-August, autumn: September-November, winter: December-February. Significant values are written in bold, significance levels: *** = p<0.001, ** = p<0.01, * = p<0.05

	Axis 1		Axis 2		Axis 3	
Eigenvalue	0.45		0.21		0.12	
Temperature 7100 [°C]	**0.87**	***	0.06		0.45	
Temp spring 7100 [°C]	**0.82**	***	0.02		**0.52**	*
Temp summer 7100 [°C]	**0.83**	***	-0.01		**0.51**	*
Temp autumn 7100 [°C]	**0.57**	**	0.21		**0.55**	*
Temp winter 7100 [°C]	-0.34		**0.48**	*	0.10	
Precipitation 7100 [mm a^{-1}]	**-0.88**	***	0.08		-0.40	
Prec spring 7100 [mm a^{-1}]	**-0.83**	***	0.12		-0.32	
Prec summer 7100 [mm a^{-1}]	**-0.80**	***	0.09		-0.44	
Prec autumn 7100 [mm a^{-1}]	**-0.93**	***	0.06		-0.36	
Prec winter 7100 [mm a^{-1}]	**-0.85**	***	0.04		**-0.47**	*
Summer days 7108 [days > 25°C a^{-1}]	**0.86**	***	-0.06		0.43	
Frost days 7109 [days < 0°C a^{-1}]	**0.59**	**	-0.26		0.03	
Flood days 0509 [days a^{-1}]	-0.30		-0.43		-0.40	

Table 2.3: Species with significant indicator values of the IndVAL-Analysis for the wet meadows of the five study sites (in Wörlitz no wet meadows were sampled). IndVAL of 1 = perfect indication, Significance levels: ***= p<0.001, **= p<0.01, *= p<0.05

Position	Site	Species	IndVAL	
1	Bleckede	*Leontodon autumnalis*	1.00	**
		Poa pratensis	0.99	**
		Stellaria palustris	0.97	*
		Trifolium repens	0.96	**
		Eleocharis uniglumis	0.85	**
		Iris pseudacorus	0.75	*
2	Strachau	*Rorippa austriaca*	0.92	**
		Barbarea stricta #	0.72	*
		Agrostis stolonifera	0.44	**
3	Schnackenburg	*Veronica scutellata*	1.00	**
		Alopecurus geniculatus	0.79	*
		Carex vulpina #	0.79	**
4	Fischbeck	*Deschampsia cespitosa*	0.75	**
		Taraxacum officinale agg.	0.74	*
		Rumex thyrsiflorus #	0.72	*
5	Steckby	*Urtica dioica*	1.00	**
		Cirsium arvense	0.94	**
		Glechoma hederacea	0.86	**
		Equisetum palustre	0.67	*

According to Burkart (2001) typical flood meadow species (river corridor plant)

Species with a rather continental as well as species with a rather oceanic distribution were evenly distributed across the wet meadows of western and eastern sites (t-tests: rather continental distributed species: $t = 1.3$, $p = 0.21$; rather oceanic distributed species: $t = -1.5$, $p = 0.14$, Fig. 2.5). Further, river corridor plants were evenly distributed in wet meadows along the gradient ($F_{4, 15} = 1.7$, $p = 0.21$; Fig. 2.2c).

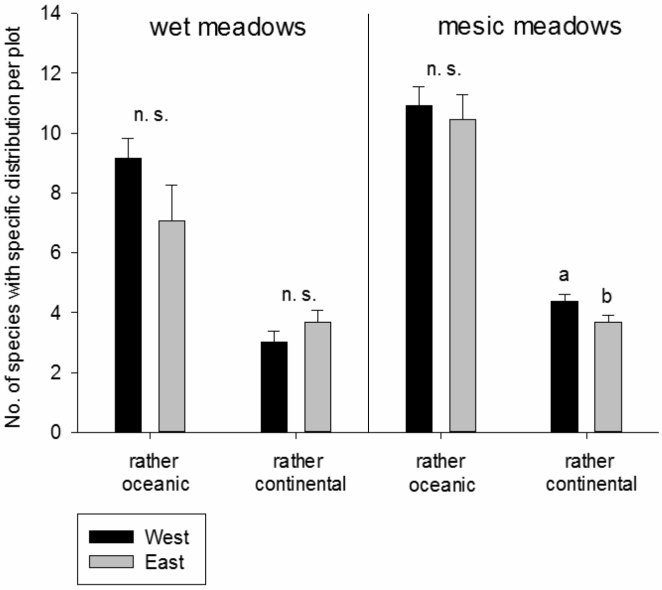

Fig. 2.5: Number of species with a 'rather oceanic' or 'rather continental' distribution per plot of wet and mesic meadows (means + SE) in the western (locations 1-3) and eastern (locations 4-6) part of the gradient.

Mesic meadows

The plots of the mesic meadows of the six sites were not arranged in the DCA ordination according to their geographic location (gradient length of first DCA axis: 3.1; total inertia: 2.8; Fig. 2.6). Nonetheless, there were significant correlations between the first three axes of the DCA and the environmental variables (Table 2.4). The plots of the western-most site 1 and the site 3 were located together on the left hand side of the first axis in the ordination graph. Characteristic species of site 1 were *Cardamine pratensis*, *Ranunculus auricomus* agg., *Plantago lanceolata*, and *Trifolium pratense* according to the IndVAL-analysis (Table 2.5), which were also plotted together in the top left corner of the DCA ordination (Fig. 2.6). In the bottom left corner *Lotus pedunculatus*, *Leontodon autumnalis*, *Symphytum officinale*, and *Vicia cracca* were plotted, which were characteristic for site 3 according to the IndVAL-analysis (Table 2.5). The plots of the other four sites grouped together on the right hand side of the first axis and the characteristic species for these sites according to the IndVAL-analysis were spread together across the right side of the ordination plot (Fig. 2.6).

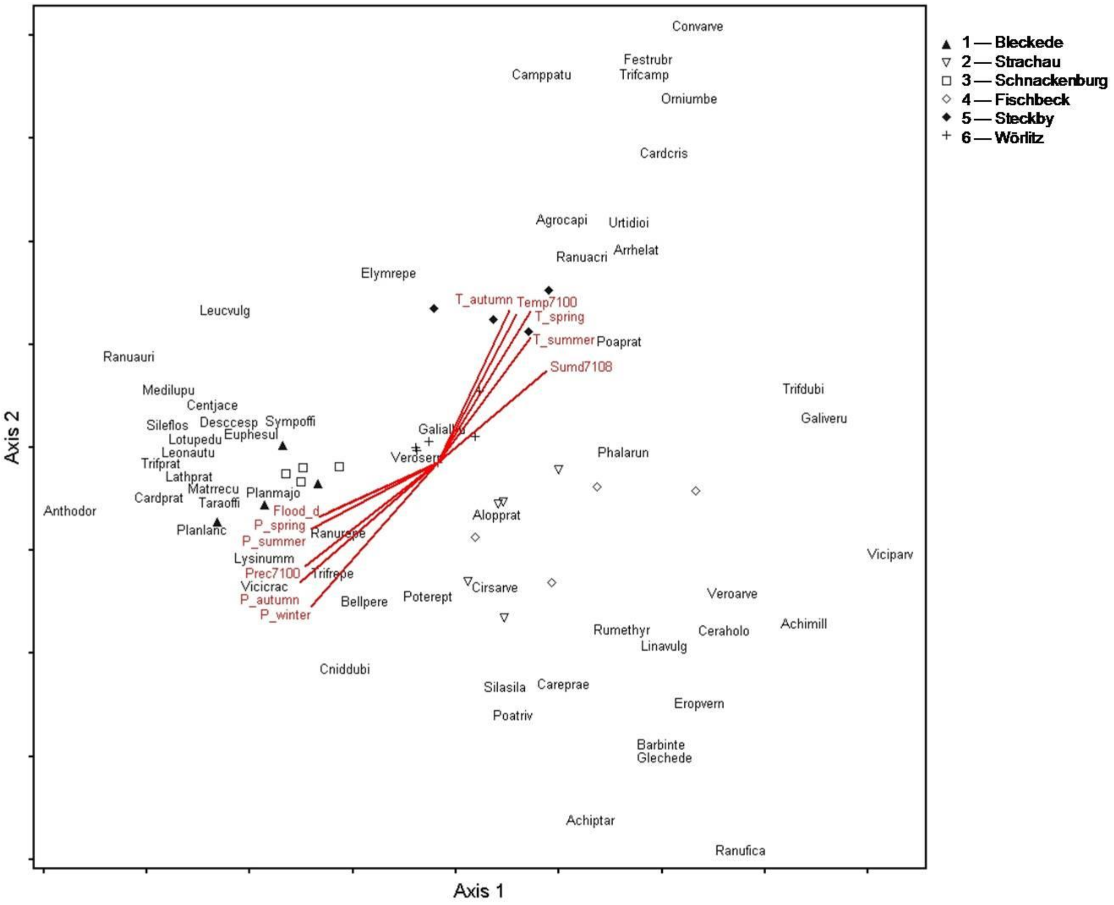

Fig. 2.6: DCA ordination tri-plot of the mesic meadows based on the abundance of 58 plant species of 26 vegetation plots, total inertia: 2.8; axis 1: eigenvalue 0.43, gradient length 3.1 SD; axis 2: eigenvalue 0.23, gradient length 2.3 SD. For abbreviations of environmental variables: see Table 2.2. For acronyms of species: see Appendix 2.1.

Table 2.4: Correlation coefficients between mesic meadow's DCA sample scores of the first three axes and environmental variables. For abbreviations of environmental variables: see Table 2, significant values are written in bold, significance levels: ***= p<0.001, **= p<0.01, *= p<0.05

	Axis 1		Axis 2		Axis 3	
Eigenvalue	0.43		0.23		0.16	
Temperature 7100 [°C]	**0.44**	*	**0.60**	**	-0.32	
Temp spring 7100 [°C]	**0.47**	*	**0.61**	**	-0.35	
Temp summer 7100 [°C]	**0.48**	*	**0.55**	**	**-0.41**	*
Temp autumn 7100 [°C]	**0.42**	*	**0.61**	**	-0.06	
Temp winter 7100 [°C]	-0.03		-0.03		**0.65**	***
Precipitation 7100 [mm a^{-1}]	**-0.57**	**	**-0.50**	**	**0.55**	**
Prec spring 7100 [mm a^{-1}]	**-0.54**	**	-0.36		**0.59**	**
Prec summer 7100 [mm a^{-1}]	**-0.56**	**	**-0.40**	*	**0.54**	**
Prec autumn 7100 [mm a^{-1}]	**-0.58**	**	**-0.54**	**	**0.57**	**
Prec winter 7100 [mm a^{-1}]	**-0.55**	**	**-0.59**	**	**0.45**	*
Summer days 7108 [days > 25°C a^{-1}]	**0.51**	**	**0.47**	*	**-0.54**	**
Frost days 7109 [days < 0°C a^{-1}]	0.34		0.07		**-0.77**	***
Flood days 0509 [days a^{-1}]	**-0.51**	**	-0.35		0.16	

Correlations of temperature- and precipitation-variables with the first DCA-axis were much smaller for mesic compared to wet meadows. For mesic meadows, the highest correlation value was found between the days of frost and the third DCA axis. Although the positioning of the locations in the DCA ordinations of the mesic meadows did not resemble the actual geographic patterns (Fig. 2.6), the IndVAL-analysis detected characteristic species for each location, which were also common meadow species (Table 2.5).

Species with a rather oceanic distribution were evenly distributed across the mesic meadows of western and eastern sites (t = -0.5, p = 0.65), while species with a rather continental distribution were more abundant on the western mesic meadows (t = -2.1, p = 0.04, Fig. 2.5). River corridor plants were more abundant in the western sites compared to the eastern sites ($F_{5, 20}$ = 9.8, p < 0.0001; differences between sites see in Fig. 2.2c).

Table 2.5: Species with significant indicator values of the IndVAL-Analysis for the mesic meadows of the six study sites. IndVAL of 1 = perfect indication, Significance levels: ***= p<0.001, **= p<0.01, *= p<0.05

Position	Site	Species	IndVAL	
1	Bleckede	*Cardamine pratensis*	0.93	**
		Ranunculus auricomus agg.	0.79	**
		Plantago lanceolata	0.74	**
		Trifolium pratense	0.57	*
2	Strachau	*Erophila verna*	0.80	**
		Linaria vulgaris	0.80	**
		Glechoma hederacea	0.66	*
		Barbarea intermedia	0.60	*
		Achillea ptarmica	0.59	*
		Poa trivialis	0.51	*
		Cnidium dubium #	0.39	*
3	Schnackenburg	*Lotus pedunculatus*	1.00	**
		Leontodon autumnalis	0.95	**
		Silene flos-cuculi	0.76	**
		Symphytum officinale	0.75	*
		Vicia cracca	0.46	*
4	Fischbeck	*Achillea millefolium*	0.90	**
		Trifolium dubium	0.74	**
		Vicia parviflora	0.71	*
		Galium verum	0.57	*
5	Steckby	*Campanula patula*	1.00	**
		Trifolium campestre	1.00	**
		Ornithogalum umbellatum	1.00	**
		Festuca rubra	0.96	**
		Agrostis capillaris	0.54	*
		Arrhenatherum elatius	0.50	*
6	Wörlitz	*Galium album*	0.49	*
		Poa pratensis	0.30	**

According to Burkart et al. (2001) typical flood meadow species (river corridor plant)

Discussion

The changing vegetation patterns of wet meadows along the gradient of the Middle Elbe suggest that climate has an effect on the distribution of vegetation in this habitat type. A relation between species composition and climatic variables was also detected in other studies for wet (Botta-Dukát et al. 2005; Hájek et al. 2008; Zelnik and Carni 2008) and semi-dry grasslands (Illyés et al. 2007). Correlations between temperature and precipitation and the vegetation patterns of wet meadows were especially pronounced. Further, the fact that correlations of temperature and precipitation variables with the first DCA-axis were larger in wet compared to mesic meadows indicate that climatic variables had a greater impact on the species composition of wet (more frequently flooded) than mesic (less frequently flooded) meadows. This result fits with Toogood et al. (2008) who argue that plant communities adapted to a dynamic water regime may be more responsive to other environmental factors than communities associated with more stable hydrologic conditions. Accordingly, a grassland community with frequent flooding responded faster to abandonment than a grassland community with a lower water table and less frequent flooding (Joyce 1998). Therefore we assume that the wet meadows of our study may be more responsive to climatic changes than the mesic meadows.

Generally, species typical for floodplain meadows of stream corridors (so called river corridor plants) tend to have a relatively continental distribution (Burkart 2001; Botta-Dukát et al. 2005). Interestingly, these species were either evenly distributed (wet meadows) or more abundant in the western sites of the studied gradient (mesic meadows). Only a few were listed as being characteristic for the vegetation records of the studied sites (Table 3 and 5). This finding supports considering the distribution of river corridor plants not to be primarily influenced by climatic variables. Therefore these species may be less vulnerable to climatic changes than species of zonal habitats (given these climatic changes occur in the range of the studied gradient). Further, topographic variability or soil heterogeneity i.e. microclimatic heterogeneous conditions might be relevant to mediate negative impacts of climatic change. Some studies suggest that microclimatic heterogeneity may buffer against large scale climatic changes (Fridley et al. 2011; Lenoir et al. 2013).

A major challenge in investigating the influence of climate along a linear structure in the landscape, such as a river, is that probably also other factors change along this gradient. In our study, land use history may be of major importance: We reduced the influence of recent land use by investigating only those meadows which were usually mown twice annually, but the land use history is rather complicated: Our sites were located on both sides of the former border between the German Democratic Republic (GDR; sites 2 — Strachau, 4 — Fischbeck, 5 — Steckby, and 6 — Wörlitz) and the Federal Republic of Germany (FRG sites 1 — Bleckede and 3 — Schnackenburg) until Germany´s reunification in 1990. In both states an intensification of agriculture took place after 1950, but a collectivisation of land in the former GDR resulted in especially large acreages and highly intensive land use (Hundt 2007). This intensive land use could have reduced species diversity (Wesche et al. 2012; Krause and Culmsee 2013) and the abundance of species typical for floodplain grasslands, because many of these species are sensitive to intensified land use (Krause et al. 2011). Therefore, the historical land use may be the reason why we recorded a higher proportion of river corridor species with a rather continental distribution in mesic meadows in the western part of the studied gradient, which was probably always moderately used. Further, this might be the reason why the mesic plots of sites 1 and 3 (formerly FRG) are plotted in the ordination together on the left site (Fig. 2.6). Land use is generally a factor that should be included in studies concerning ecosystems that evolved under anthropogenic land use (e.g. Bütof et al. 2012).

Conclusions

It remains uncertain whether the vegetation patterns of wet meadows that we found were caused by climatic or by other underlying factors along the gradient. The vegetation patterns along the gradient cannot be detected by means of presence or absence of plant species as only a few species are at their range limits in this geographical area. Instead, different abundances of common meadow species were causing the vegetation patterns along the gradient. Typical floodplain meadow species, the so called river corridor plants and relevant species from a nature conservation point of view, are relatively evenly distributed along the river or probably due to land use history more abundant in the western part of the gradient. Concerning climate change, we therefore assume that typical floodplain meadow species are less vulnerable to direct climatic changes than species of zonal habitats, as long as these climatic changes do not exceed the range of the climatic gradient today. Especially when management is kept at an optimal level for the target communities and species, effects of environmental changes such as climate change might be less pronounced (Bütof et al. 2012; Speed et al. 2013). However, if the climatic changes exceed the differences found along the Middle Elbe River today, typical floodplain meadow species may be especially challenged by climatic changes as dispersal limitations from one suitable habitat to another (from one river corridor to the next) are likely.

We further presume that the total assemblage of common and typical floodplain meadow species of wet meadows might be more vulnerable to climate change than the vegetation of mesic meadows (as the DCA-analysis points to an influence of climate on species assemblage patterns of wet meadows). However, as we cannot be sure that our detected patterns are solely climate driven, we recommend studying longer geographic gradients to evaluate the influence of climate also covering the distribution range of climatically indicative species.

Aside from that, environmental changes that are indirectly related to climate change such as water level changes due to altered discharge regimes caused by altered precipitation patterns in the catchment are very likely to affect common and typical floodplain species and the whole floodplain ecosystem more severely than direct climatic changes.

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Appendix:

Appendix 2.1: List of the species found in this study with acronyms of DCA-ordinations and continentality classes assigned by BiolFlor (Kühn et al. 2004); Species marked with # are typical flood meadow species (river corridor plant) according to Burkart et al. (2001)

No.	Species	Acronyme of DCA-ordinations	Continentality class of BIOLFLOR
1	*Achillea millefolium*	Achimill	no class assigned
2	*Achillea ptarmica*	Achiptar	os
3	*Agrostis capillaris*	Agrocapi	os
4	*Agrostis stolonifera*	Agrostol	sos
5	*Alisma plantago-aquatica*	Alisplan	no class assigned
6	*Allium vineale*	not included in DCA	os
7	*Alopecurus geniculatus*	Alopgeni	os
8	*Alopecurus pratensis*	Alopprat	sks
9	*Anthoxanthum odoratum*	Anthodor	os
10	*Arctium lappa*	not included in DCA	sos
11	*Arrhenatherum elatius*	Arrhelat	os
12	*Barbarea intermedia*	Barbinte	o
13	*Barbarea stricta* #	Barbstri	ks
14	*Bellis perennis*	Bellpere	os
15	*Bromus hordeaceus*	not included in DCA	os
16	*Calystegia sepium*	not included in DCA	os
17	*Campanula patula*	Camppatu	sos
18	*Cardamine pratensis*	Cardprat	os
19	*Carduus crispus*	Cardcris	no class assigned
20	*Carex acuta*	Careacut	ks
21	*Carex praecox* #	Careprae	sk
22	*Carex vulpina* #	Carevulp	os
23	*Centaurea jacea*	Centjace	sos
24	*Cerastium dubium* #	not included in DCA	sk
25	*Cerastium glomeratum*	not included in DCA	os
26	*Cerastium holosteoides*	Ceraholo	no class assigned
27	*Cirsium arvense*	Cirsarve	no class assigned
28	*Cnidium dubium* #	Cniddubi	sks
29	*Convolvulus arvensis*	Convarve	no class assigned
30	*Cuscuta europaea* #	not included in DCA	sks

No.	Species	Acronyme of DCA-ordinations	Continentality class of BIOLFLOR
31	*Daucus carota*	not included in DCA	os
32	*Deschampsia cespitosa*	Desccesp	no class assigned
33	*Eleocharis uniglumis*	Eleounig	ks
34	*Elymus repens*	Elymrepe	ks
35	*Equisetum palustre*	not included in DCA	sos
36	*Equisetum pratense*	not included in DCA	ks
37	*Erophila verna*	Eropvern	os
38	*Euphorbia esula*	Euphesul	sks
39	*Festuca pratensis*	not included in DCA	os
40	*Festuca rubra*	Festrubr	sos
41	*Galium album*	Galialbu	os
42	*Galium aparine*	not included in DCA	os
43	*Galium boreale* #	not included in DCA	ks
44	*Galium palustre*	Galipalu	os
45	*Galium uliginosum*	not included in DCA	no class assigned
46	*Galium verum*	Galiveru	no class assigned
47	*Glechoma hederacea*	Glechede	os
48	*Glyceria fluitans*	not included in DCA	os
49	*Glyceria maxima*	Glycmaxi	no class assigned
50	*Holcus lanatus*	not included in DCA	os
51	*Hypericum perforatum*	not included in DCA	sos
52	*Iris pseudacorus*	Irispseu	os
53	*Lamium album*	not included in DCA	os
54	*Lamium purpureum*	not included in DCA	os
55	*Lathyrus palustris* #	Lathpalu	no class assigned
56	*Lathyrus pratensis*	Lathprat	no class assigned
57	*Leontodon autumnalis*	Leonautu	os
58	*Leucanthemum vulgare*	Leucvulg	os
59	*Linaria vulgaris*	Linavulg	sos
60	*Lolium perenne*	not included in DCA	so
61	*Lotus pedunculatus*	Lotupedu	o
62	*Lysimachia nummularia*	Lysinumm	so
63	*Lysimachia vulgaris*	Lysivulg	no class assigned
64	*Matricaria recutita*	Matrrecu	sos
65	*Medicago lupulina*	Medilupu	no class assigned
66	*Mentha arvensis*	Mentarve	no class assigned
67	*Myosotis scorpioides*	Myosscor	sos
68	*Oenanthe aquatica*	not included in DCA	sos
69	*Ornithogalum umbellatum*	Orniumbe	so
70	*Persicaria amphibia*	Persamph	no class assigned
71	*Phalaris arundinacea*	Phalarun	no class assigned
72	*Phragmites australis*	not included in DCA	no class assigned
73	*Picris hieracioides*	not included in DCA	sks
74	*Plantago lanceolata*	Planlanc	os
75	*Plantago major*	Planmajo	no class assigned
76	*Poa palustris*	Poapalu	sks
77	*Poa pratensis*	Poaprat	no class assigned
78	*Poa trivialis*	Poatriv	os
79	*Potentilla reptans*	Poterept	os
80	*Ranunculus acris*	Ranuacri	os
81	*Ranunculus auricomus*	Ranuauri	no class assigned
82	*Ranunculus ficaria*	Ranufica	os
83	*Ranunculus flammula*	Ranuflam	os
84	*Ranunculus repens*	Ranurepe	no class assigned
85	*Rorippa amphibia*	not included in DCA	ks
86	*Rorippa anceps* #	Roriance	so
87	*Rorippa austriaca* #	Roriaust	sk

No.	Species	Acronyme of DCA-ordinations	Continentality class of BIOLFLOR
88	*Rumex acetosa*	not included in DCA	no class assigned
89	*Rumex crispus*	Rumecris	os
90	*Rumex obtusifolius*	not included in DCA	os
91	*Rumex thyrsiflorus* #	Rumethyr	ks
92	*Sanguisorba officinalis* #	not included in DCA	ks
93	*Silaum silaus* #	Silasila	sos
94	*Silene flos-cuculi*	Sileflos	os
95	*Sisymbrium loeselii*	not included in DCA	ks
96	*Sium latifolium*	Siumlati	sos
97	*Stachys arvensis*	not included in DCA	o
98	*Stachys palustris*	Stacpalu	no class assigned
99	*Stellaria media*	not included in DCA	no class assigned
100	*Stellaria palustris*	Stelpalu	ks
101	*Symphytum officinale*	Sympoffi	os
102	*Taraxacum officinale*	Taraoffi	no class assigned
103	*Trifolium campestre*	Trifcamp	os
104	*Trifolium dubium*	Trifdubi	os
105	*Trifolium hybridum*	not included in DCA	sos
106	*Trifolium pratense*	Trifprat	os
107	*Trifolium repens*	Trifrepe	no class assigned
108	*Tripleurospermum perforatum*	not included in DCA	os
109	*Urtica dioica*	Urtidioi	no class assigned
110	*Valerianella locusta*	not included in DCA	os
111	*Veronica arvensis*	Veroarve	os
112	*Veronica chamaedrys*	not included in DCA	os
113	*Veronica scutellata*	Veroscut	os
114	*Veronica serpyllifolia*	Veroserp	os
115	*Vicia angustifolia*	not included in DCA	os
116	*Vicia cracca*	Vicicrac	no class assigned
117	*Vicia lathyroides*	not included in DCA	so
118	*Vicia parviflora*	Viciparv	o

CHAPTER 3

DIFFERENTIAL EFFECTS OF REDUCED WATER POTENTIALS ON THE GERMINATION OF FLOODPLAIN GRASSLAND SPECIES INDICATIVE OF WET AND DRY HABITATS

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Abstract:

Floodplain meadow ecosystems are characterized by high water level fluctuations and highly variable soil water potentials. Additionally, climate change scenarios indicate an increasing risk for summer drought along the northern Upper Rhine and the Middle Elbe River, Germany. While adult plants often persist even after strong changes in water availability, early life phases such as seed germination and seedling establishment might be more vulnerable. Therefore we tested (i) whether reduced soil water potentials will affect the germination of meadow species and whether the response varies between (ii) forbs indicative of wet and dry habitats or (iii) seeds originating from the rivers Elbe and Rhine. We exposed seeds of 20 floodplain meadow species with different moisture requirements from five plant families to a water potential gradient ranging from 0 to -1.5 MPa. While across species germination percentage and synchrony decreased, germination time increased at reduced water potentials. Germination of the species indicative of dry habitats decreased more strongly, was slower, and less synchronous at reduced water potentials than that of species indicative of wet habitats. Seeds from the rivers Elbe and Rhine did not differ in their germination characteristics. We propose that species of wet sites follow an all-or-nothing-strategy with fast and synchronous germination to maximize competitive advantages betting on a high probability of moist conditions for establishment (optimists). In contrast, species from dry sites appear to follow a bet-hedging strategy with a moisture-sensing mechanism for unsuitable conditions (pessimists) resulting in a slower and less synchronous germination.

Keywords:

alluvial meadows * climate change * Ellenberg values * flood meadows

Introduction

Survival and persistence of plant populations strongly depend on reproduction, thus seed germination and seedling establishment are the most critical stages in the life of plant individuals (Grubb 1977, Kitajima and Fenner 2000). Without successful germination and establishment, populations are threatened by extinction. Germination processes are affected by the biotic environment e.g. by competition from the established vegetation (Bakker and de Vries 1992, Kitajima and Fenner 2000), or by a litter layer (e.g. Jensen and Gutekunst 2003, Loydi et al. 2013), and by abiotic environmental conditions. In case of the latter, temperature and water availability are the main abiotic drivers of germination processes (Baskin and Baskin 2001, Fenner and Thompson 2005). Most species require specific environmental conditions for the germination process and these factors are decisive for the subsequent seedling establishment (Baskin and Baskin 2001).

Floodplain grasslands are hydrologically highly dynamic ecosystems and characterised by the interplay of wet conditions during regularly or irregularly occurring floods and dry conditions over the summer (Hölzel and Otte 2001). In directly inundated (functional) floodplains this gives rise to highly variable soil water potentials in time (i.e. within years) and space (i.e. along flooding gradients) resulting in a distinct zonation of plant communities (Leyer 2005) which is also determined by seed and germination traits (Leyer and Pross 2009). Due to the tightly intermingled vegetation zones, species density is high and floodplains harbor many rare and endangered species (Donath et al. 2003, Toogood et al. 2008). However, species-rich floodplain meadows declined strongly over the last centuries due to habitat losses mainly caused by land use changes (e.g. Wesche et al. 2012), river regulations (e.g. Tockner and Stanford 2002), and river training (Brunotte et al. 2009). Consequently, these meadows are of high conservation value and protected by the Habitats Directive (92/43/EEC, habitat type 6440: Alluvial meadows of river valleys of the *Cnidion dubii*) and subject to various restoration measures (Donath et al. 2007, Schmiede et al. 2012).

Climate change might pose an additional threat to the persistence of species-rich floodplain meadows. Regional climate change projections indicate higher temperatures and an increasing risk for summer droughts for the late 21st century due to less summer precipitation in western and northern Germany in relation to the reference period 1961-1990 (Jacob et al. 2008, Görgen et al. 2010). Accordingly, reduced river discharges during summers are projected for the large rivers Rhine (Görgen et al. 2010) and Elbe (Conradt et al. 2012). This, in turn, would lower the water-table in the adjacent floodplain with negative effects on the soil water potential. In combination with increased transpiration at higher temperatures, these changes could induce severe drought-stress in plants of floodplain meadows (Jensen et al. 2011). Additionally, increased temperatures could affect seed longevity, a prelude for building up viable seed banks (Ooi 2012). As temperature and water availability are important drivers for the germination process, their changes will very likely affect this early stage in plant life (Walck et al. 2011). Consequently, species abundance and population dynamics might be altered leading to distribution shifts or extinctions (Thuiller et al. 2005). To estimate future distribution and abundance of plant species, it is essential to gain knowledge on their specific requirements for seedling recruitment (e.g. Adler and HilleRisLambers 2008, Walck et al. 2011).

Recently, the impact of climate change on vegetation has received increasing attention. Different experimental approaches have already been conducted focusing on CO_2 (e.g. Edwards et al. 2001, Rasse et al. 2005), temperatures (e.g. Klanderud and Totland 2005, Hudson et al. 2011) or precipitation (e.g. Yahdjian and Sala 2002, Beier et al. 2012) and their effects on single species or plant communities. Some greenhouse and common garden experiments simulated drought (e.g. Jentsch et al. 2011, Weisshuhn et al. 2011) or flooding scenarios (e.g. van Eck et al. 2006). While all of these approaches focused on the matured plant, little work has been done considering the early life stages. Here, one possible approach is to investigate germination at different water availabilities with seeds exposed to different water potentials (e.g. Fyfield and Gregory 1989, Swagel et al. 1997, Akhalkatsi and Lösch 2001). To date, most studies in which water potentials were manipulated focused on germination traits of single plant species whereas comparative studies on a larger number of species are scarce (but see Evans and Etherington 1990). Moreover, rare plant species and the influence of hydrological factors on their germination have only rarely been investigated (but see Geißler and Gzik 2008a) and, to our knowledge, only one study investigated whether germination differs between species indicative of different habitats (Evans and Etherington 1990). However, analyzing the responses of plant functional groups based on key life-history traits to climatic changes appears to be a promising approach (Ooi 2012).

Therefore, the objective of our study was to test how floodplain meadow species, preferring contrasting habitats with respect to soil moisture, respond (in terms of germination) to different water potentials. We exposed seeds of 20 floodplain meadow species to a water potential gradient ranging from no water limitation to the permanent wilting point. The overall aim was to understand possible impacts of climate change on the early life stage of floodplain meadow plants. We also included seeds of five of these species from populations at the Elbe River to test the effect of seed origin on germination characteristics. To include different aspects of the germination of species, we analyzed (i) germination percentage, (ii) mean germination time and (iii) synchrony of germination. Germination percentage simply measures the recruitment success of a batch of seeds and population fitness increases with increasing germination. In contrast, the success of recruitment is not necessarily monotonically increasing with mean germination time or synchrony. Rather, the benefit of early or late germination (i.e. low or high germination time) and germination in one batch or scattered germination over time (i.e. high and low synchrony) may vary with environmental context.

Our research questions and hypotheses were:

1) Do reduced water potentials affect the germination patterns of all plant species? We hypothesize that all study species show reduced germination percentages at reduced water potentials. Further, we expect that germination will take longer and will be less synchronous at reduced water potentials.

2) Does the temperature regime affect germination? We expect germination time to decrease with increasing temperature.

3) Do seeds originating from populations at the Elbe differ in their response to reduced water potentials compared to those from populations along the Rhine? We expect germination of seeds from the River Elbe, where annual precipitation is lower, to be more successful at reduced water potentials than germination of seeds from the Rhine.

4) Does seed germination of floodplain plant species indicative of wet habitats differ to those floodplain plant species indicative of dry habitats? We hypothesize seed germination of plants indicative of wet habitats to decrease more strongly, to be slower and less synchronous at reduced water potentials than that of plants indicative of dry habitats.

Methods

Study species

We selected 20 species (four from each of five plant families) occurring in floodplain grasslands along the Rhine River (Table 3.1). These species consist of typical and rare floodplain meadow plants, such as *Galium boreale, Pseudolysimachion longifolium* or *Peucedanum officinale* (according to Burkart 2001) and more common and widespread grassland species, such as *Plantago media, Linaria vulgaris* or *Galium verum*. Moisture requirements of the study species were classified according to the Ellenberg indicator value for moisture (Ellenberg et al. 1992). Moisture indicator values of the selected species varied from 3 (indicative of dry habitats) to 9 (indicative of wet habitats). We sought to include pairs of genetically related species with different preferences for soil moisture to attain a phylogenetically balanced design. Plant nomenclature follows Wisskirchen and Haeupler (1998).

Seed collection

Seeds from 13 out of the 20 species were hand-collected from autochthonous populations in floodplain meadows along the northern Upper Rhine, Germany (49°50'N 8°25'E – 49°51'N 8°23'E). The seeds of six species (*Filipendula ulmaria, F. vulgaris, Linaria vulgaris, Plantago media, Sanguisorba minor, Veronica teucrium*) were obtained from a commercial supplier (Rieger & Hoffmann GmbH, Blaufelden-Raboldshausen, Germany) due to insufficient amounts of seeds from natural populations along the Rhine River. Seeds of *Galium palustre* originated from floodplain meadows at the Middle Elbe, Germany, (52°32'N 11°59'E – 52°49'N 12°03'E) as seeds of this species could not be found at the Rhine River nor ordered from a commercial supplier. Hand-collected seeds were sampled between August and October 2010 depending on species-specific seed maturation. Freshly matured seeds were collected from at least two populations of a minimum of 20 individuals. For comparing the germination characteristics of seeds from the Rhine with seeds from the Elbe, seeds of five species (*Centaurea jacea, Galium verum, Inula britannica, Pseudolysimachion* *longifolium, Silaum silaus*) were additionally collected in autumn 2010 at the Middle Elbe (52°32'N 11°59'E – 52°49'N 12°03'E). These seeds were also collected from at least two populations of at least 20 individuals (with the exception of *Silaum silaus* from which only one population was available).

Table 3.1: Study species with information on plant family, Ellenberg indicator value for moisture (EIV moist, ind = species with "indifferent behavior"), indicated habitat, seed viability (%) and germination capacity under outdoor conditions (%)

Species	Family	EIV moist	Ind. habitat	Viability (%) [a]	Germination capacity (%) [b]
Pimpinella saxifraga	Apiaceae	3	dry	98.0 ± 1.2	78.0 ± 2.3
Peucedanum officinale #		4	dry	96.7 ± 1.4	20.0 ± 5.3
Selinum carvifolia		7	wet	99.0 ± 1.0	99.3 ± 0.7
Silaum silaus #		ind	-	100.0 ± 0.0	91.3 ± 4.4
Inula salicina	Asteraceae	6	-	91.5 ± 1.4	84.0 ± 4.0
Inula britannica #		7	wet	94.0 ± 1.2	76.0 ± 5.0
Centaurea jacea		ind	-	90.0 ± 1.2	77.3 ± 3.7
Serratula tinctoria		ind	-	89.5 ± 2.5	84.0 ± 1.2
Veronica teucrium	Plantaginaceae	3	dry	98.0 ± 2.0	72.7 ± 0.7
Linaria vulgaris		4	dry	60.0 ± 12.0	60.7 ± 10.7
Plantago media		4	dry	86.0 ± 2.0	79.3 ± 5.8
Pseudolysimachion longifolium #		8	wet	88.0 ± 1.6	85.3 ± 2.7
Filipendula vulgaris	Rosaceae	3	dry	94.0 ± 2.0	72.7 ± 8.5
Sanguisorba minor		3	dry	70.0 ± 2.0	51.3 ± 8.2
Sanguisorba officinalis #		7	wet	92.6 ± 1.9	94.7 ± 2.4
Filipendula ulmaria		8	wet	50.0 ± 2.0	61.3 ± 5.2
Galium verum	Rubiaceae	4	dry	89.2 ± 2.3	49.3 ± 1.8
Galium album		5	-	96.0 ± 1.0	78.7 ± 2.9
Galium boreale #		6	-	89.0 ± 2.5	24.7 ± 8.5
Galium palustre		9	wet	56.0 ± 3.4	18.7 ± 0.7

According to Burkart (2001) typical flood meadow species (river corridor plants)
[a] Tetrazolium chloride test with 25 seeds per replicate (n=2)
[b] tested in common garden, 50 seeds per replicate (n=3)

The area along the northern Upper Rhine where the seeds were sampled receives a mean annual precipitation of 643 mm and a mean annual temperature of 10.6 °C (1981-2010 Gernsheim, DWD). The area at the middle Elbe receives a lower mean annual precipitation of 555 mm and a mean annual temperature of 9.0 °C (1981-2010 Boizenburg; DWD).

Seed handling and germination tests

After collection, seeds were manually cleaned, air-dried and stored in darkness at room temperature (app. 20 °C) until the start of the experiment in December 2010. Viability of seeds was tested for each population (25 per replicate, n=2) with a 1% tetrazolium chloride solution.

To test the germination capacity under outdoor conditions, seeds were sown into trays (50 per replicate, n=3) with sterile standard garden soil and placed in a common garden (50°32‘12”N 8°41’35”E, 172 m a.s.l.) at the same time as the climate chamber experiment started. The sowing date in January 2011 ensured cold wet stratification. Seeds were watered regularly and seedlings were counted and removed at least every other week for two years.

Experimental design

We used a factorial experimental design to study the effects of *species* (20 species), *water potential* (0, -0.25, -0.5, -1.0, -1.5 MPa), and *temperature* (day/night: 15/5 °C and 20/10 °C) on seedling emergence. Each treatment combination (species x temperature x water potentials) was replicated five times, resulting in 1000 experimental units. Additionally, for the comparison of the germination patterns of seeds from the Rhine River with those of seeds from the Elbe River the seeds of the above mentioned five species from the Elbe were also treated in five replicates with the five water potentials (0, -0.25, -0.5, -1.0, -1.5 MPa) at both temperatures (15/5 °C and 20/10 °C) resulting in another 250 Petri dishes.

We used the osmotic agent mannitol (Euro OTC Pharma GmbH, Bönen, Germany) to establish defined water potentials. Mannitol concentrations of 0.1, 0.2, 0.4, and 0.6 mol l^{-1} were prepared to generate water potentials of approximately -0.25, -0.5, -1.0, and -1.5 MPa, respectively (according to Swagel et al. 1997). As a control (full water availability = water potential of 0 MPa) we used distilled water.

Fifty seeds of each species (25 seeds of *Peucedanum officinale,* due to its large seed size) were placed in sterile Petri dishes with one piece of filter paper moistened with 3 mL of D-mannitol solution or distilled water. In order to reduce evaporation five Petri dishes were sealed together in a plastic bag.

As a stratification measure the seeds were exposed to cold wet conditions for five weeks in climate chambers (Rumed type 3401, Rubarth Apparate GmbH) at 5 °C to ensure breaking of potential seed dormancy. For incubation, we exposed the seeds to 12 h light and 12 h darkness and two diurnally fluctuating temperatures (15/5 °C and 20/10 °C) to simulate different spring temperature conditions.

Germination was defined as protrusion of the radicle. Germination was checked twice a week and seedlings were removed. After 4 weeks of incubation, germination decreased and Petri dishes were checked only once a week. While checking the Petri dishes for seedlings, the amount of mannitol solution in the Petri dishes was controlled. In order to keep osmotic potentials constant during the experiment, Petri dishes were carefully washed with 7.5 mL of mannitol solution or distilled water (control), emptied and re-filled with 3 mL of new mannitol solution or distilled water after four weeks of incubation. After 8 weeks of incubation the experiment ended since almost no further germination was observed.

Germination parameters

As response variables, we calculated the germination percentage (%), mean germination time (days) and synchrony of germination (an index ranging from 0-1, unitless) per replicate (according to Ranal and Santana 2006, Ranal et al. 2009). The germination percentage is the percentage of all germinated seeds from the initial number of seeds. Mean germination time and synchrony of germination were calculated based on seedling counts over time (Ranal et al. 2009). Mean germination time is a measurement of the weighted average length of time required for germination (Ranal and Santana 2006). The unit depends on the counting frequency and is days in this study. The mean germination time $\bar{t}$ is:

$$\bar{t} = \sum_{i=1}^{k} n_i t_i \Big/ \sum_{i=1}^{k} n_i$$

where t_i is the time from the start of the experiment to the i^{th} observation day and n_i is number of seeds germinated in the i^{th} time, and k is the last time of germination (for detail see Ranal et al. 2009).

The synchrony of germination indicates the germination variability over time, ranging from 0 to 1 (high values indicate highly synchronous germination). The synchrony of germination Z is:

$$Z = \sum C n_{i},_{2} / N \qquad C n_{i},_{2} = n_i(n_i - 1)/2 \qquad N = \sum n_i\left(\sum n_i - 1\right)/2$$

where n_i is number of seeds germinated in the i^{th} time.

Data handling and statistical analyses

For data analysis, plants with an Ellenberg moisture value of 3 or 4 were classified as indicators of dry habitats, and species with a moisture value of 7, 8, or 9 as indicators of wet habitats. Species with an intermediate Ellenberg moisture value of 5 or 6 or a so called indifferent behavior towards moisture (see Ellenberg et al. 1992) were not included in the comparison between these two groups of species in our study.

For most species the osmotic threshold for germination was -1.0 or at least -1.5 MPa (see Fig. 3.1). To avoid zero inflation, the osmotic potentials of -1.0 and -1.5 MPa had to be omitted from the analyses. Moreover, we had to exclude the results of *Galium palustre,* due to the extremely low germination percentage of the seeds of this species in the climate chamber experiment (1.0 ± 0.5 %).

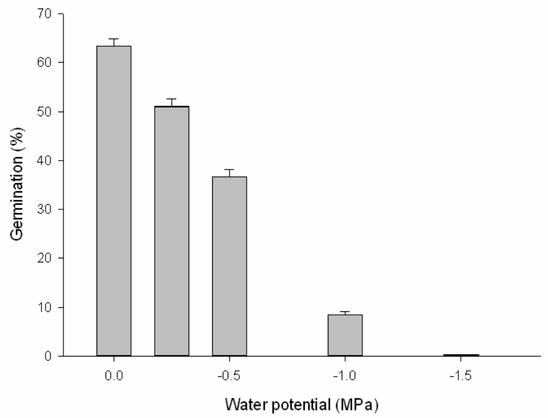


Fig. 3.1: Germination percentage at the tested water potentials (mean + SE); including all treatments and species.

The effects of the experimental predictor variables *species*, *water potential*, and *temperature* on germination percentage, germination time and synchrony of germination were analyzed by three-way ANOVAs. To account for inherent effects of family identity we first calculated one-way ANOVAs with the factor *plant family* for every transformed (see below) response variable (germination percentage ($F_{4, 565} = 39.6$, $p < 0.001$), germination time ($F_{4, 565} = 80.3$, $p < 0.001$) and synchrony of germination ($F_{4, 565} = 51.4$, $p < 0.001$) and used the residuals for the three-way ANOVAs. As a measure of the relative contribution of each factor and interaction to the total variability in germination percentage, germination time and synchrony of germination, we used the ratio of the sum of squares of the factor or interaction of interest to the total sum of squares (i.e. variance contribution (vc) for all factors, their interactions and the error). Following the three-way ANOVA, we conducted (i) Tukey HSD-tests for the interaction of *species* x *water potential* to analyze whether reducing the water potential to -0.25 and -0.5 MPa affected the seed germination percentages on the species level and (ii) contrast analyses to analyze if the species indicative of wet and dry habitats differ in their response to reduced water potential conditions. For the contrast analyzes, the germination responses (germination percentage, germination time and synchrony of germination) of the seeds from species indicative of wet habitats were tested against the germination responses of the seeds from species indicative of dry habitats separately for the water-potentials -0.25 and -0.5 MPa (but not for the non-stress control conditions).

For the analysis of the effects of seed origin (Rhine *vs.* Elbe) on the germination parameters, we conducted ANOVAs with the factors *species*, *water potential*, *temperature* and *origin*.

Data were transformed to approximate normal distribution and variance homogeneity (germination percentage: arcsin (square root/100); mean germination time and synchrony: log+1). All statistical tests were conducted using STATISTICA 10 (StatSoft Inc.).

Results

General characteristics of seed material

Viability (%) of the seeds was generally high (Table 3.1). Most species had >85% viable seeds, exceptions were *Filipendula ulmaria* (50 ± 2%), *Galium palustre* (56 ± 3%), *Linaria vulgaris* (60 ± 12%), and *Sanguisorba minor* (70 ± 2%). Under outdoor conditions 13 species had germination percentages of >70%, whereas low germination percentages were exhibited by *Galium boreale* (24 ± 9%), *Galium palustre* (19 ± 1%), and *Peucedanum officinale* (20 ± 5%, Table 3.1).

Germination in response to water-potential, temperature, and origin

Generally, germination percentage was significantly reduced at lower water potentials and totally ceased at a water potential of -1.5 MPa (Fig 3.1).

The three-way ANOVA indicated that germination percentage varied significantly among *species*, this factor explained 41% of the total variation (vc; Table 3.2). Furthermore, germination percentage was significantly influenced by the *water potential* (vc = 30%; Table 3.2). At a water potential of -0.5 MPa, the germination of most study species was significantly reduced. Only the germination of four species was not susceptible to a water potential of -0.5 MPa: *Centaurea jacea, Inula britannica, Sanguisorba minor,* and *S. officinalis* (*p*-values > 0.05, Fig 3.2). Mean germination time was likewise mostly influenced by the factors *species* (vc = 43%) and *water potential* (vc = 27%, Table 2). Additionally, germination time was significantly affected by the temperature regime at which the seeds germinated (vc = 12 %; Table 3.2). On average, seeds needed 13 days for germination at the temperature regime 15/5 °C and 17 days at the higher temperature regime 20/10 °C (including all species except *Galium palustre*). Synchrony of germination mainly depended on the factors *species* (vc = 35 %) whereas *water potential* explained only 11% of the total variation (Table 3.2).

The comparison of seed germination of five species originating from the Rhine and the Elbe River indicated species-specific responses. *Species* identity explained the largest part of the total variation in germination percentages ($F_{4,\,240}$ = 299.8, p < 0.001, vc = 48 %). The main factor of interest, i.e. *origin*, had no effect on the germination percentages ($F_{1,\,240}$ = 0.04, p = 0.85). Further, the response to the reduced water potential did not differ between origins as no interaction between *origin* and *water potential* was detected ($F_{2,\,240}$ = 0.71, p = 0.49). Species also explained most of the variation in mean germination time ($F_{4,\,239}$ = 742.1 p < 0.001, vc = 60 %). Although *origin* had a significant effect on germination time, it only explained a small part of variation ($F_{1,\,239}$ = 145.8, p < 0.001, vc = 3 %). No *origin* x *water potential* interaction was found for germination time ($F_{2,\,239}$ = 1.1, p = 0.35). Again in the analysis of synchrony *species* explained most of the variation ($F_{4,\,239}$ = 198.4 p < 0.001, vc = 51 %) while *origin* had a significant, but small impact ($F_{1,\,239}$ = 31.9, p < 0.001, vc = 2 %) and no *origin* x *water potential* interaction was found ($F_{2,\,239}$ = 1.3, p = 0.27).

Table 3.2: Results of the ANOVA for the climate chamber experiment: Effects of *species*, *water potential* and *temperature* on germination (%), mean germination time (days), and synchrony of germination; including the water potentials 0, -0.25, and -0.5 MPa; *df* = degrees of freedom, *F* = variance ratio, *p* = error probability, vc (%) relative contribution of individual factors and their interactions to total variance;

		Germination (%)			**Mean germination time**			**Synchrony**		
	df	***F***	***p***	**vc (%)**	***F***	***p***	**vc (%)**	***F***	***p***	**vc (%)**
species (S)	18	76.9	<0.0001	40.9	106.0	<0.0001	42.9	38.7	<0.0001	35.0
temperature (T)	1	<0.1	0.9527	0.0	532.6	<0.0001	12.0	34.4	<0.0001	1.7
water potential (WP)	2	504.4	<0.0001	29.8	608.3	<0.0001	27.4	110.6	<0.0001	11.1
S x T	18	9.3	<0.0001	5.0	7.4	<0.0001	3.0	9.3	<0.0001	8.4
S x WP	36	8.8	<0.0001	9.4	3.8	<0.0001	3.1	6.6	<0.0001	12.0
T x WP	2	4.2	0.0153	0.3	0.6	0.5346	0.0	0.2	0.8226	0.0
S x T x WP	36	1.2	0.2517	1.2	1.8	0.0037	1.5	4.8	<0.0001	8.8
error	456			13.5			10.3			22.9
Contrasts: wet vs. dry species										
WP -0.25 MPa		63.5	<0.0001		2.3	0.1316		9.4	0.0023	
WP -0.5 MPa		71.6	<0.0001		5.1	0.0246		0.1	0.7199	

Wet versus dry habitat species

Contrast analyses revealed that the seeds of species indicative of wet habitats had significantly higher germination percentages than species indicative of dry habitats at reduced water-potentials (see Table 3.2 and Fig. 3.3a). On average, 77 % ± 3 % (mean ± SE, N = 50) of the seeds from species of wet habitats germinated at water potentials of -0.25 MPa versus only 62 % ± 3 % (N = 80) of the seeds from species of dry habitats. At water potential -0.5 MPa, 61 % ± 4 % (N = 50) of the seeds from species of wet habitats germinated versus only 44 % ± 3 % (N = 80) of the seeds from species of dry habitats. Besides, the seeds of the species from dry habitats needed approx. two days longer for germination at a water potential of -0.5 MPa (see Table 3.2 and Fig. 3.3b) and germinated slightly less synchronously at a water potential of -0.25 MPa (see Table 3.2 and Fig. 3.3c) than the seeds of the species from wet habitats.

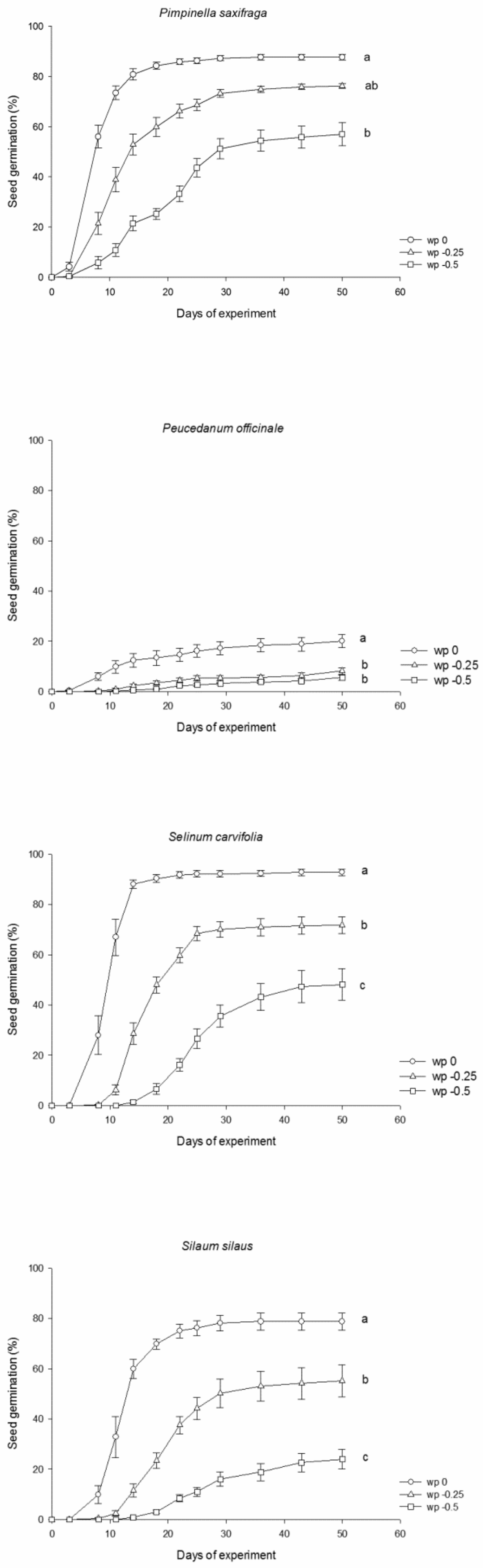
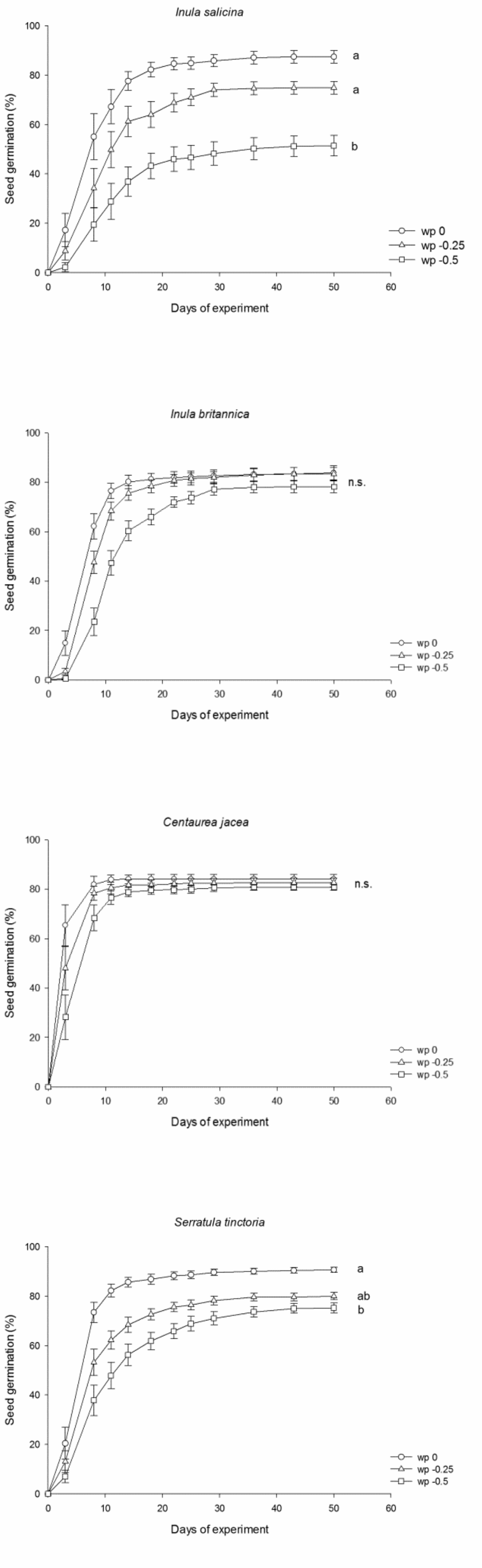


Fig. 3.2 (continued, caption at the end)



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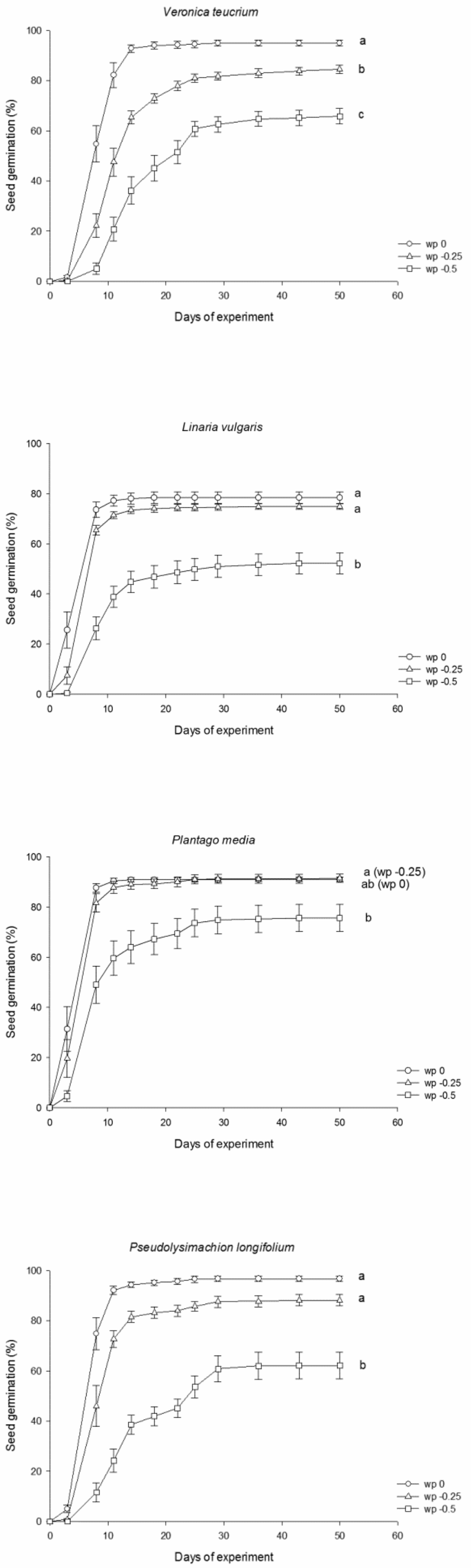

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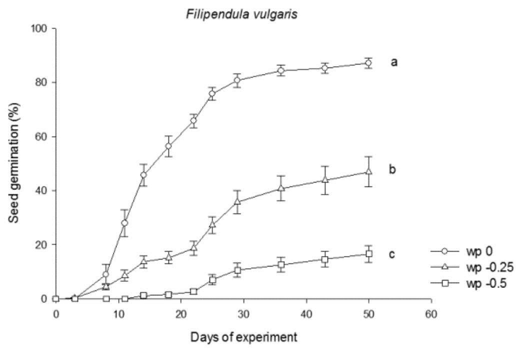

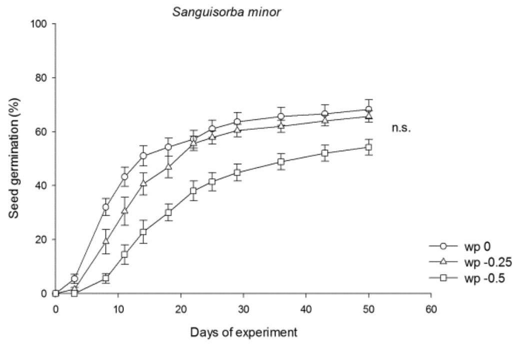

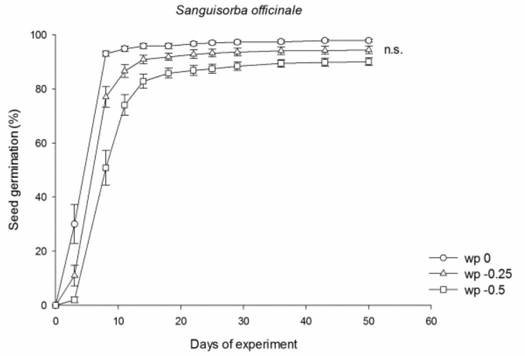

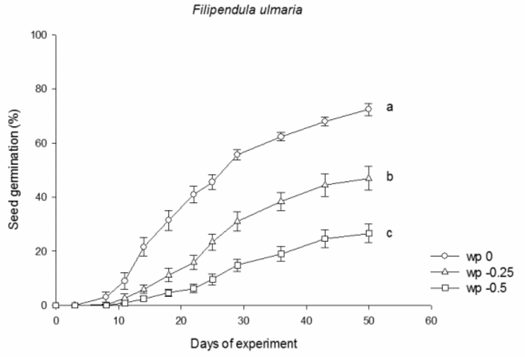

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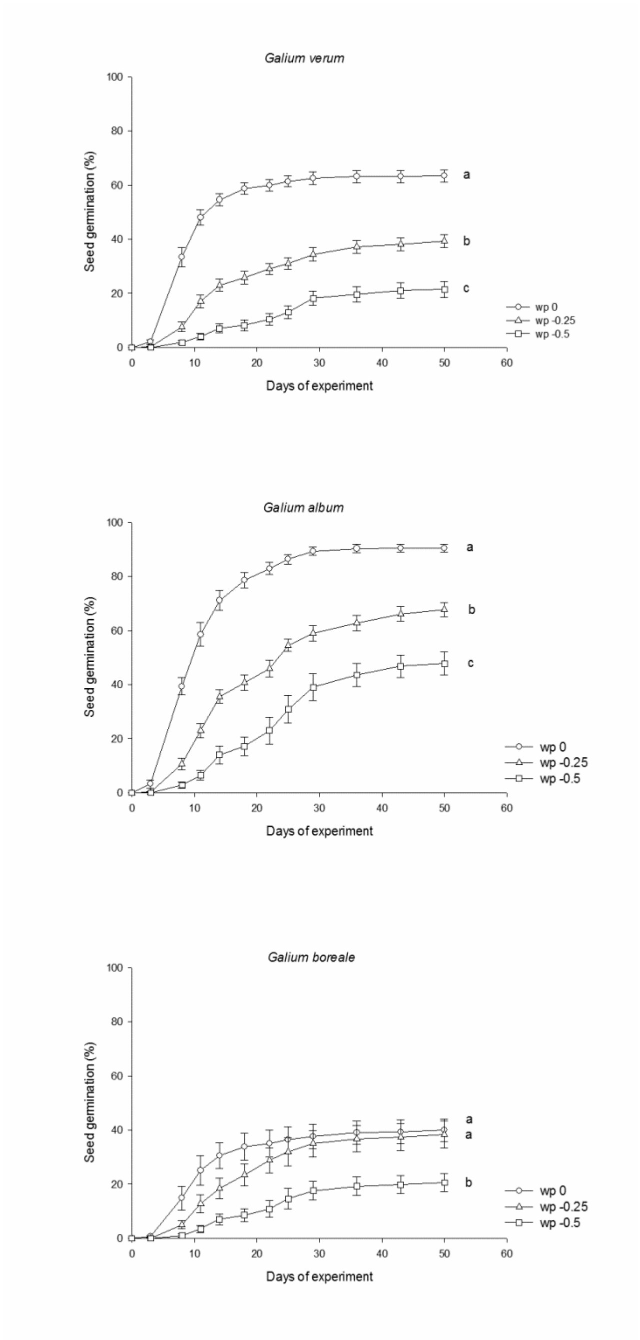

Fig. 3.2: Cumulative germination percentage over time of the study species (except *Galium palustre*), averaging the data of the two temperature regimes (mean ± SE). Species order in accordance to Table 1. Different letters indicate differences in the final germination percentage between water potential treatments (0, -0.25 and -0.5 MPa).

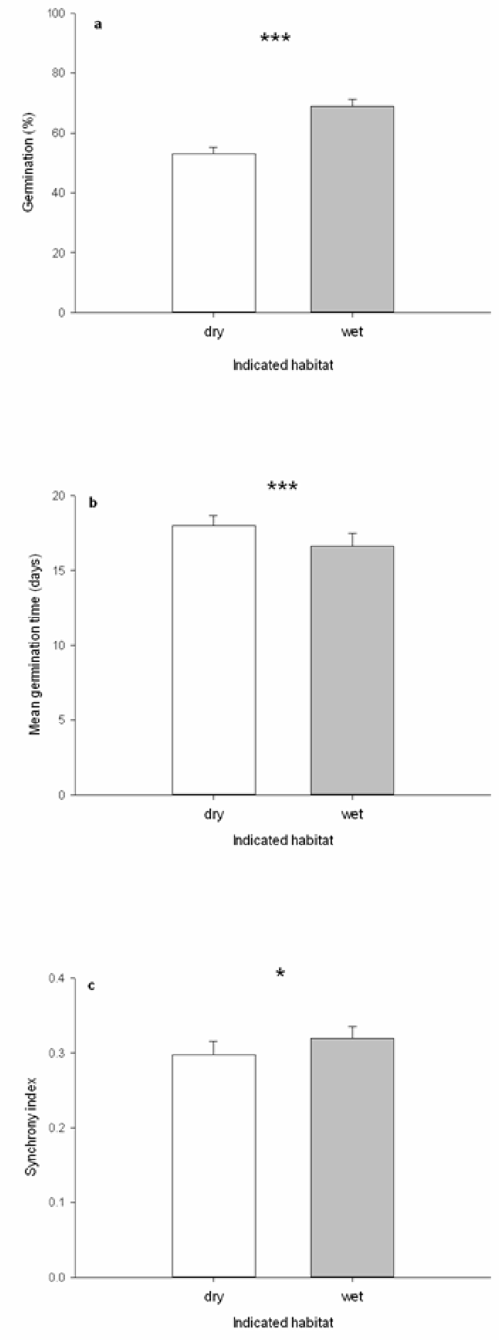

Fig. 3.3: Germination percentage, germination time and synchrony, averaging the data of the two temperature regimes (mean + SE) of the species indicative of dry (*Pimpinella saxifraga, Peucedanum officinale, Veronica teucrium, Linaria vulgaris, Plantago media, Filipendula vulgaris, Sanguisorba minor, Galium verum)* and wet (*Selinum carvifolia, Inula britannica, Pseudolysimachion longifolium, Sanguisorba officinalis, Filipendula ulmaria)* habitats including the water potenitals -0.25 and -0.5 MPa (excluding *Galium palustre*), significance levels:* = $p < 0.05$, *** = $p < 0.001$.

Discussion

Germination responses

In accordance with our first hypothesis, the germination of all species was negatively affected by reduced water availability and almost ceased at a water potential of -1.5 MPa. This emphasizes the importance of soil moisture as a key requisite for the germination process (Baskin and Baskin 2001) and is in line with other studies in which germination was affected by low water potentials (Evans and Etherington 1990, Swagel et al. 1997, Akhalkatsi and Lösch 2001, Springer 2005, Daws et al. 2008). Two of these studies included species that were able to germinate at reduced water potentials (for details see Evans and Etherington 1990, Springer 2005). Also in our study it is surprising that germination of four species (*Centaurea jaceae, Inula britannica, Sanguisorba minor*, and *S. officinalis*) was unaffected by a water potential as low as -0.5 MPa. A further seven species germinated to an equal percentage at water potential -0.25 MPa compared to the control conditions (*Galium boreale, Inula salicina, Linaria vulgaris, Pimpinella saxifraga, Plantago media, Pseudolysimachion longifolium, Serratula tinctoria*). Germination time and synchrony of germination were also influenced by the water-potential in our study. This finding corresponds to other studies in which a delayed onset of germination was reported at reduced water potentials (Evans and Etherington 1990, Daws et al. 2008).

While the three response variables were mainly influenced by species identity (which fits with Burmeier et al. 2010) followed by water potential (see results of the three-way ANOVA, Table 2), it has to be acknowledged that all response variables were affected by plant family. Concerning germination time, an accumulation of species with the ability of very fast germination (< 24 h) within certain plant families was recently reported in a review on this topic (Parsons 2012). It seems that fast germination may be especially abundant in high stress habitats as, for example, functional floodplains (Parsons 2012). Overall, we can conclude that germination characteristics are species-specific and partly phylogenetically determined.

The seeds of most species germinated faster at the lower temperature (15/5 °C), therefore we have to reject our second hypothesis. Probably the lower temperature regime corresponds better to the temperature conditions of meadow habitats during spring under temperate climates, the season in which many floodplain meadow species usually germinate (Hölzel and Otte 2004). Additionally, seed germination probably avoids warmer periods when increased evaporation may cause decreased water availability for seedlings. In two studies on Australian plant species, optimum germination temperatures coincides with the average summer or winter temperatures of the local habitats (Jurado and Westoby 1992, Cochrane et al. 2011), but only in one study the preferred germination seasons in the field is suggested to be the winter (Cochrane et al. 2011). Furthermore, studies on species of semi-arid grasslands document that the water potential is less limiting when germination temperature is close to the optimum (Romo et al. 1991, Qi and Redmann 1993). In our study on species of temperate grasslands, however, no significant interaction between temperature and water potential was found for the response variable germination time (see Table 2). Concerning potential climate change effects, faster seed germination at lower temperatures could result in an earlier onset of germination, since overall higher future temperatures are projected for Germany (Jacob et al. 2008). A shift to earlier germination may ensure moist germination conditions, as increases in precepitation in early spring are projected (Jacob et al. 2008). However, this may also lead to new threats for the seedlings, such as an increased mortality risk caused through spring floods during periods of suitable germination temperature.

Germination of seeds from the Rhine and Elbe Rivers

The germination of seeds from the Elbe River was surprisingly similar to the germination of the seeds from the Rhine River. Differences in germination between species were by far larger than between the populations from the two rivers. This is further evidence that germination characteristics are species-specific. Maybe from a seed's perspective the rivers Elbe and Rhine are not so different. Both floodplains are more or less regularly inundated and are dry during summer. These features may be more important than the mean annual precipitation or temperature. Further, higher mean annual temperature at the Rhine River might lead to similar water-potentials in the soils due to a higher evapo-transpiration despite higher annual amount of precipitation. Due to the large similarity in germination between seeds of the two origins it can be assumed that our findings for the tested species at the river Rhine are transferable to other Central European floodplain ecosystems with similar climatic conditions.

Germination responses of species indicative of wet and dry habitats

We hypothesized that germination of plant species indicative of wet habitats will decrease more at reduced water potentials than that of species indicative of dry habitats as we expected species from dry habitats to be better able to cope with drier conditions. Strikingly, we found the opposite. Selection pressures for responding to the moisture status of their environment might be low for species indicative of wet habitats. Thus, under experimental conditions, they even germinate under conditions unfavorable for successful establishment, which is a rare situation in their habitat *in situ*. Another environmental factor (i.e. temperature) might be more important for their germination. In turn, seeds of species indicative of dry habitats are probably capable of sensing the moisture status of their environment, thereby avoiding germination under unfavorable conditions in the field. The results of Evans and Etherington (1990) are in contrast to what we found; in their study wetland species did not germinate to a great extent at low water potentials, but some dry habitat species germinated successfully under dry conditions. Still, they concluded that the "inability" to germinate under dry conditions might be a dormancy mechanism to avoid the failure of seedling establishment. In our study, however, all seeds were cold-wet stratified to ensure breaking of dormancy prior to the experiment. Germinating under dry conditions could easily lead to the death of the seedling as the probability that water availability increases again is rather low in dry habitats. Hence, the selection pressure towards moisture-sensing mechanisms might be high in dry habitats to respond to the right window of opportunity for successful germination.

Germination time of species indicative of dry habitats was longer than that of species indicative of wet habitats. We speculate that it needs some time for seeds of species from dry habitats to sense the actual environmental conditions in their surroundings, while seeds of species from wet habitats germinate immediately. This fits with the finding that the seeds of species indicative of wet habitats germinate more synchronously than the seeds of species indicative of dry habitats, although the absolute difference between groups was small and only significant for the water potential -0.25 MPa. Also the difference in germination time between the two groups of species is rather small (the seeds of species from wet habitats germinated approx. two days earlier than the seeds from species indicative of dry habitats) at the water potential -0.5 MPa. It remains unclear if this finding is ecologically relevant under field conditions. Nevertheless, especially in the productive wet meadows, early germination could be advantageous for establishment. This corresponds to a study on the germination of 91 species in response to a temperature gradient where species of productive grassland germinated rapidly (Olff et al. 1994). Therefore, we assume that the species of wet sites follow an all-or-nothing-strategy with fast and synchronious germination to maximize competitive advantages and betting on a high probability of moist conditions for establishment ("optimists"). In contrast, species of dry sites follow a bet-hedging strategy with a moisture-sensing mechanism for the right conditions betting on a high probability for unsuitible conditions ("pessimists" *sensu* Jones 1992 who coined this terminology for strategy types of photosynthetic reactions on drought stress) resulting in a slower and less synchronous germination.

Conclusions

The germination of almost all studied species was decreased by lower water potentials, which strengthens the results of former studies (Evans and Etherington 1990, Swagel et al. 1997, Akhalkatsi and Lösch 2001, Springer 2005, Daws et al. 2008) and demonstrates that floodplain meadow species will be negatively influenced in their earliest life stage (i.e. seed germination) by decreasing water availabilities during future climate change. However, the species indicative of wet and of dry habitats of floodplain meadows might be differently affected. Our experimental data suggest that seeds of species indicative of dry habitats show sensitivity to the moisture status of their immediate environment. Their 'pessimistic' response (germinating only when they sense sufficient moist conditions) probably enables them to track the time windows with high probability for successful germination and establishment. Seeds of species indicative for wet habitats do not possess such a mechanism since the conditions in their typical habitat are usually sufficiently moist. Their 'optimistic' response to this environmental factor probably makes them comparably vulnerable to climate change. Shifts of these species further down the elevation gradient in floodplains (where conditions are still moist enough for successful establishment) might be the consequence. Further, faster seed germination under low temperatures could also lead to a shift to earlier germination, where the soil is still moist from precipitation during winter and spring. Then other factors, such as the occurrence or timing of spring floods or frosts may gain importance. More research is needed concerning the timing of germination under changing climatic conditions.

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Conflict of interest

None.

CHAPTER 4

EFFECTS OF REDUCED SUMMER PRECIPITATION ON THE FORAGE QUANTITY AND QUALITY OF FLOODPLAIN MEADOWS AT THE ELBE AND THE RHINE RIVER

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Submitted to *PLOS One*

Abstract

Floodplain meadows along rivers are semi-natural habitats and depend on regular land-use. When used non-intensively, they offer suitable habitats for many (including rare) plant species. Floodplains are hydrologically dynamic ecosystems with both periods of flooding and of dry conditions. In German floodplains, dry periods may increase due to reduced summer precipitation as projected by climate change scenarios. Against this background, the question arises, how the forage quantity and quality of these meadows might change in future.

We report results of two field trials that investigated effects of experimentally reduced summer precipitation on hay quantity and quality of floodplain meadows at the Rhine River (2011-2013) and at two Elbe tributaries (2009-2011). We measured the amount of hay biomass, its contents of crude protein, crude fibre, energy, fructan, nitrogen, phosphorus, and potassium.

The annual yield decreased under precipitation reduction at the Rhine River. In the first cut in June, quantity and quality of the hay were almost not affected by the experiments at both rivers. At the Rhine River, biomass of the second cut in September decreased under the precipitation reduction treatments and contents of nitrogen and crude protein in the hay increased. At the Elbe River, hay quantity and quality in the second cut was only marginally affected by the treatments.

We conclude that the yield of floodplain meadows may become less reliable in future since the annual yield decreased under precipitation reduction at the Rhine River. However, the first and agriculturally more important cut was almost unaffected by the precipitation reduction, which is probably due to sufficient soil moisture from winter/spring. As long as the water levels of the rivers will not decrease during spring in future, at least the use of the hay from the first cut of floodplain meadows appears sustainable under future climate change.

Keywords

Alluvial meadow * climate change * hay meadow * nitrogen deposition

Introduction

European semi-natural habitats such as agriculturally unimproved grasslands make a large contribution to the biodiversity of landscapes (Billeter et al. 2008, Liira et al. 2008). This is not only due to the high plant species richness, which is characteristic for semi-natural grasslands, but also due to large numbers of animal species (e.g. insects and birds) for which grasslands offer suitable habitats (e.g. Hendrickx et al. 2007). Hotspots of biodiversity are floodplain grasslands along large lowland rivers, which are the outcome of typical flooding regimes and long lasting land use practices with moderate intensity (Seffer et al. 2008). Floodplain grasslands also harbour many rare plant species (Donath et al. 2003, Toogood et al. 2008) e.g. typical river corridor plants such as *Cnidium dubium*, *Thalictrum flavum* or *Viola elatior* (Burkart 2001). Due to the impact of flooding events in combination with dry conditions over the summer, floodplains are highly dynamic environments (Hölzel and Otte 2001). Floodplains are mainly used as grasslands for grazing (pastures) and mowing (meadows) to gain fodder for domestic livestock. Mowing once or twice annually without fertilizer application is recommended for facilitating a high species richness (Seffer et al. 2008).

As other semi-natural grasslands in Europe, floodplain meadows also strongly declined over the last centuries and especially decades. The main causes of losses for species rich floodplain meadows are the reduction of the dynamic hydrologic conditions due to river regulations (Tockner and Stanford 2002) or river training (Brunotte et al. 2009), and land use changes as intensification (e.g. Wesche et al. 2012) or abandonment (e.g. Jensen and Schrautzer 1999). Consequently, these meadows are of high conservation value and certain types of meadows found in European floodplains are protected by the Habitats Directive (92/43/EEC, habitat type 6440: Alluvial meadows of river valleys of the *Cnidion dubii*; 6510: Lowland hay meadows) and subject to various restoration measures (Jensen et al. 2006, Donath et al. 2007, Schmiede et al. 2012).

If biodiversity targets are to be integrated into grassland management systems, the yield of low input species-rich grasslands has to be known (Isselstein et al. 2005). It is an ongoing nature conservation concern how the biomass of these non-intensively managed meadows can be incorporated into agricultural land use systems (Donath et al. 2004, Isselstein et al. 2005). Undoubtedly, it is preferable to integrate these meadows into farming systems instead of just managing them in the framework of nature conservation schemes. In future, however, the productivity of semi-natural grasslands may be affected by increased rainfall variability due to climate change.

Precipitation is one of the most influential abiotic factors for plant productivity (Huxman et al. 2004). Changes in precipitation patterns are projected to occur in the course of climate change (IPCC 2007). For Germany, regional climate change projections indicate higher temperatures and an increasing risk for summer droughts for the late 21st century due to less summer precipitation in relation to the reference period 1961-1990 (Jacob et al. 2008, Görgen et al. 2010). Accordingly, river discharges during summers are projected to decrease, e.g. at the large rivers Rhine (Görgen et al. 2010) and Elbe (Conradt et al. 2012).

This, in turn, could lower the water table in the adjacent floodplains with negative effects on the soil water potential. In combination with increased transpiration at higher temperatures, these changes could induce drought stress in plants of floodplain meadows (Jensen et al. 2011). Plant responses to drought stress are manifold: including decreased cell elongation and reduced photosynthesis, the responses generally lead to reduced plant growth and delayed plant development (Hsiao and Acevedo 1974).

In recent years, some climate change experiments were conducted in grassland ecosystems, e.g. in a semi-arid steppe (Yahdjian et al. 2006), in mesic tallgrass prairies (Fay et al. 2000), and in temperate grasslands (Grime et al. 2000, Bloor et al. 2010, Bütof et al. 2012, Walter et al. 2012). Only one of these studies focused on how forage quality – the ecosystem service relevant to farmers – might change in the future using the example of nitrogen and protein content of the biomass (Walter et al. 2012). Still, additional variables relevant for farmers such as crude fibre, crude protein, energy content or fructan have not been analysed in this context. Generally, data on the forage quality of non-intensively used semi-natural grasslands are scarce in the international literature (but see Donath et al. 2004, Klaus et al. 2011). Also Tallowin and Jefferson (1999) stated in their review that "unfortunately data for hays from species-rich semi-natural lowland grasslands in the UK are lacking" and it seems that it is still a current need to examine this topic. Generally, high values of crude protein, digestible energy and contents of N, P, and K indicate high forage quality of hay while high amounts of crude fibre and fructan impair forage quality (Opitz von Boberfeld 1994).

To clarify the effects of changes in summer precipitation on the quantity and quality of the biomass of European floodplain grasslands, we conducted field experiments in which we reduced the amount of precipitation with rainout shelters. We harvested biomass, analysed its amount and the parameters crude fibre, crude protein, digestible energy, fructan and the element contents of nitrogen, phosphorus, and potassium. Further, we calculated the annual yield as the product of biomass amount and energy content. We expected the amount of biomass, its quality and the overall yield to decrease under precipitation reduction. The data we present here originate from two independent precipitation experiments, conducted at the rivers Rhine and Elbe.

We aimed at answering the following research questions: Does reduced summer precipitation affect (i) the quantity of hay, (ii) its quality in the first and second cut, and (iii) the overall annual energy yield of floodplain meadows?

Material and Methods

Experiments at the Elbe and the Rhine River

In this paper we summarise results of two precipitation reduction experiments in floodplain meadows at the Rhine River and at two Elbe River tributaries originating from two independent studies. Because the two studies were planned and conducted independently from each other, different experimental designs were employed. However, as the overall aims and the used rainout shelters were identical, we present the results in this integrating paper.

Permissions

The permits for the field experiments were provided by the Biosphere Reserves Elbe River of Lower Saxony for the experiment at the Sude, from the Biosphere Reserves Elbe River of Saxony-Anhalt as well as from the Nature Conservation Authority from Saxony-Anhalt for the Havel. Permits for the experiment at the Rhine were provided from the city of Riedstadt, regional council Darmstadt and forestry administration of Hesse.

Study areas and study sites

The studies were conducted on floodplain meadows belonging to the functional floodplain (not disconnected from the river and thus inundated in times of high water) at the Rhine River and at two Elbe River tributaries, the Havel and the Sude River. All studied floodplains have in common that the climatic and hydrological conditions result in highly variable soil water potentials: while winter, spring and early summer may bring floods, the summer periods are notably dry (especially the continental Havel site in the Elbe region and the Rhine site). Along with the strong seasonal and inter-annual fluctuations of the water level of the rivers, the groundwater tables also fluctuate strongly (Elbe: Leyer 2005; Rhein: Bissels et al. 2005).

The study area at the Rhine River is situated in the Hessian part of the Holocene floodplain of the northern Upper River Rhine near Riedstadt, about 30 km southwest of Frankfurt, Germany (N 49°49', E 8°26'). The climate in this area is relatively dry and warm with a mean annual precipitation of 602 mm (1961-1990 Riedstadt-Erfelden, DWD 2013) and a mean annual temperature of 9.7°C (1961-1990 Frankfurt Main airport, DWD 2013). The soils can be classified as calcic Fluvisols (Burmeier et al. 2010). The vegetation of the study site itself is relatively species poor because it was an arable field before 1983 (for details on the history of the site see Böger 1991, Bissels et al. 2004). Since 1983 the meadows are mown up to two times annually. Two sites differing in elevation were chosen as study sites (a higher/dryer site and a lower/wetter site). The species composition of the study meadow is dominated by *Festuca arundinacea*. Further frequently occurring species are *Dactylis glomerata* and *Leucanthemum vulgare* on the higher site and *Potentilla reptans* and *Symphytum officinale* on the lower site. The nomenclature of plant species follows Wisskirchen and Haeupler (1998).

The meadows at Elbe tributaries are located at the Sude River (near Sückau in Lower Saxony, N53°19' E010°57') and the Havel River (near Kuhlhausen in Saxony-Anhalt, N52°47' E012°11'). The site at the Sude River experiences rather oceanic climatic conditions with a mean annual precipitation of 663 mm and a mean annual temperature of 8.3°C (1961-1990; data from the nearest weather station in Boizenburg; DWD 2013). The site at the Havel River has on the contrary relatively continental climatic conditions with a mean annual precipitation of 503 mm (1961-1990; data from the nearest weather station in Havelberg; DWD 2013) and a mean annual temperature of 9.1°C (1976-2009; data from the nearest weather station measuring temperature in Seehausen; DWD 2013). Both sites are regularly flooded by either the Sude or the Havel River, which are first order tributaries of the Elbe River. The soils of both sites are gleyic Fluvisols which consist mainly of loamy material over sandy sediments. The active floodplains along the Sude and Havel are typically used as grasslands and the two meadows are mown twice annually. Both study sites contain *Cnidium*-floodplain meadow vegetation with characteristic river corridor plants (according to Burkart 2001), such as *Cnidium dubium, Stellaria palustris* and *Carex vulpina*, and more frequently occurring species, such as *Alopecurus pratensis*, *Deschampsia cespitosa*, *Potentilla anserina*, *Potentilla reptans*, and *Ranunculus repens*.

The experiment at the Rhine River

The experiment at two sites at the Rhine River was conducted in the vegetation periods 2011 and 2012. The rainout shelters measured 3 m x 3 m and were built according to Yahdjian & Sala (2002) using acrylic glass pipes as flumes. To minimize the edge effects, the investigated plots beneath the rainout shelters were adjusted to 4 m². The two experimental factors applied were elevation above base flow (high: 320 cm above base flow; low: 240 cm above base flow) and precipitation reduction (-50 %, -25 %, no reduction). Two types of controls were used: 1) control plots with rainout-shelters where the acrylic glass pipes were turned upside down (to test the rainout-shelter effect without rain reduction and 2) control plots without rainout shelters (see Table 4.1). Precipitation reduction was conducted from March to October. The experiment was run with three replicates. The weather conditions of the study years are shown in Fig. 4.1c.

Table 4.1: Overview of experimental treatments of the precipitation reduction experiments at the rivers Elbe and Rhine: -50 % = 50% precipitation reduction; -25 % = 25% precipitation reduction; -25 %/+N = 25% precipitation reduction and fertilization with nitrogen; +N = fertilization with nitrogen; control = controls without rainout shelters; control+shelter = controls with rainout shelters.

	-50 %	-25 %	+N /-25 %	+N	control	control+shelter
Elbe		2009-2011	2009-2011	2009-2011	2009-2011	
Rhine	2011-2012	2011-2012			2011-2012	2011-2012

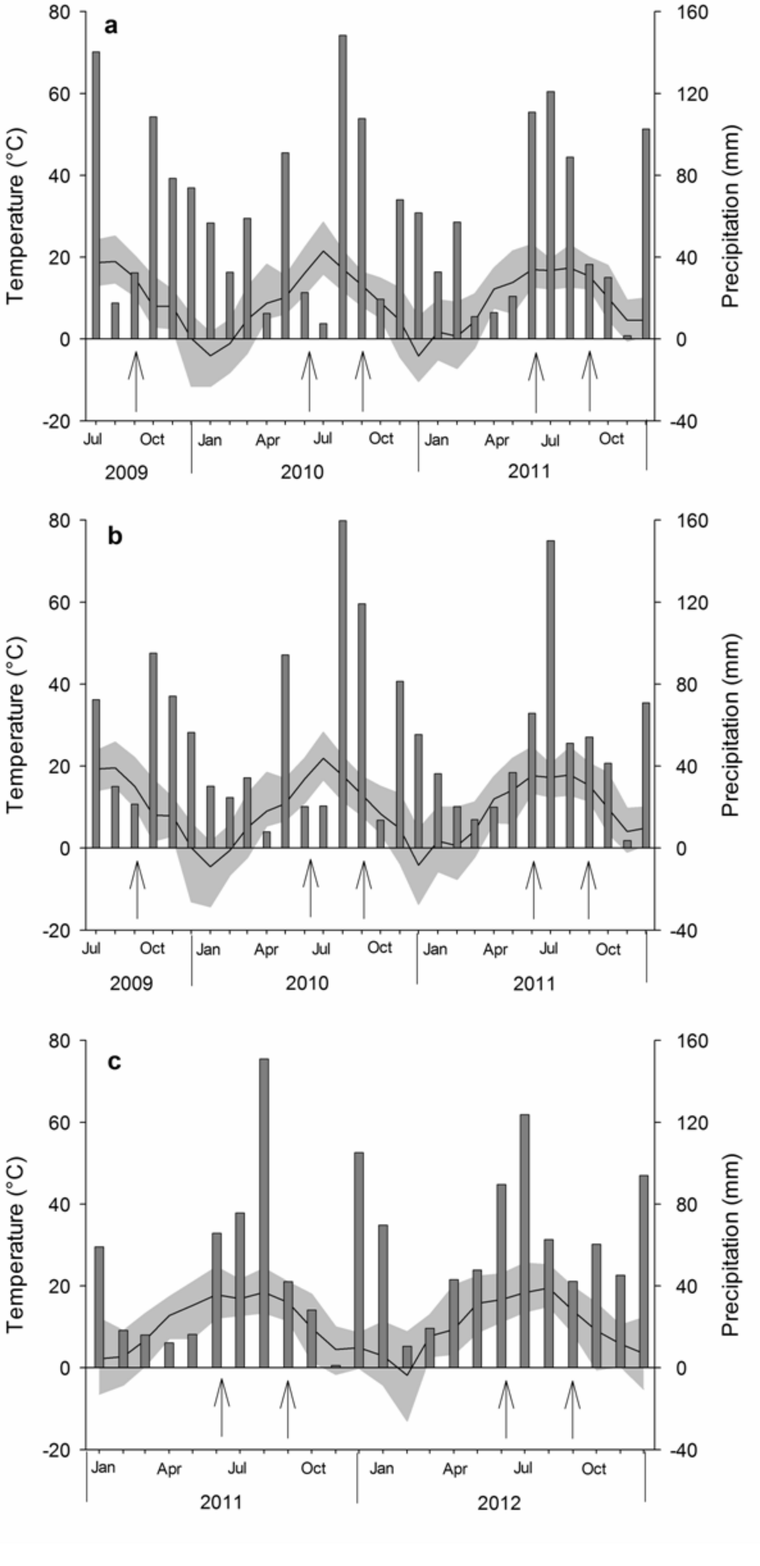

Fig. 4.1: Weather conditions at the Elbe tributaries Sude (a) and Havel (b) during the study years 2009 to 2011 and at the Rhine (c) during the study years 2011 and 2012 (data provided by the DWD 2013). The black line with grey shade represents daily average, minimal and maximal monthly temperatures. The grey bars are monthly sums of precipitation. Arrows indicate the dates of biomass sampling.

The experiment at the Elbe River

In the vegetation periods 2009 to 2011, we conducted a field experiment at the two Elbe River sites. In a two-factorial design, we manipulated summer precipitation that was reduced by approx. 25 % with rainout shelters, and nitrogen deposition that was imitated by fertilization with ammonium-nitrate (35 kg N ha^{-1} a^{-1}). Precipitation reduction and fertilization treatments were conducted from May to October (in 2009 from July to October). Fertilizer was applied at seven dates evenly distributed over this period. As in the Rhine experiments, the rainout shelters measured 3 m x 3 m and were built according to Yahdjian & Sala (2002) but using UV permeable greenhouse plastic as flumes. To minimize edge effects, study plots covered only the inner approx. 4 m² of the rainout shelter. Four treatments were implemented (see Table 1): 1.) precipitation reduction and fertilization (-25 %/+N), 2.) only fertilization (+N), 3.) only precipitation reduction (-25 %), and 4.) controls without treatments (controls). The experiment was run with seven replicates. The weather conditions of the study years are shown in Fig. 4.1a and 4.1b.

Response variables

As response variables we measured the amount of biomass (g m^{-2}), its contents of crude fibre (XF, % dry weight; dw), crude protein (XP, % dw), fructan (% dw), and the elements nitrogen (N, mg g^{-1} dw), phosphorus (P, mg g^{-1} dw), and potassium (K, mg g^{-1} dw). Energy content of the biomass was assessed as digestible energy (DE), net energy for lactation (NEL) and metabolisable energy (ME; all in MJ kg^{-1} dw). While the latter two are applicable in case of ruminants, DE is an estimate relevant for horse fodder. As these energy values are interrelated and the hay of semi-natural meadows is per se preferably used for horses in the study regions, we focus on DE in this study, but as an overview, we present the ME- and NEL-values in Table 4.2 and Appendix 4.1.

On the Elbe sites, biomass samples were taken from 0.25 m² subplots (three samples of biomass of which one was taken for the forage quality measurements and two were used for the element content measurements) in June 2010 and 2011 (first cuts) and September 2009 to 2011 (second cuts). At the Rhine sites, biomass samples were taken from 0.1 m² subplots (12 samples which were ground together and then separated for the forage quality and element content measurements) in June 2011 and 2012 (first cuts) and September 2011 and 2012 (second cuts). In autumn 2011, not enough biomass could be sampled for the fructan analysis on the plots at the Rhine. Biomass samples of Elbe and Rhine sites were dried at 60°C for three days.

Crude protein, crude fibre, energy variables, and fructan were measured with the NIRS technique (AG FUKO, Hannover, Germany). Annual yield (GJ ha^{-1}) was calculated as the product of digestible energy (DE, GJ kg^{-1} dw) and dry biomass (kg dw ha^{-1}). Nitrogen contents of the Elbe samples were measured using a CN-Analyzer (vario MAX, elementar, Hanau, Germany) and of the Rhine samples using an Auto-Analyzer (AA 3, Bran & Lübbe, Norderstedt, Germany). Potassium and phosphorus contents of the Elbe samples were measured with the ICP-OES technique (samples of 2009: Perkin Elmer ICP/OES, Perkin

Elmer, Hamburg, Germany; samples of 2010/2011: iCAP^{TM} 6300 ICP-OES Analyzer, Thermo Scientific, Germany) after digestion of the samples in a Lab microwave (MLS Start 1500, Leutkirch, Germany). The Rhine samples were dry ash combusted and afterwards phosphorus contents were measured photometrically (Spectrophotometer, Zeiss, Jena, Germany) and potassium contents were measured using an Atomic Absorption Spectrometer (AAS-Varian 220 FS, Varian, Darmstadt, Germany).

Data handling and statistical analyses

Due to the differences in study design at the Elbe and Rhine River, both data sets were analysed individually. The effects of the predictor variables on the response variables (amount of biomass, crude protein, crude fibre, digestible energy, fructan, N-content, P-content, and K-content) were tested with repeated measures ANOVAs (with study year as the within subject factor) separately for the data from the first and the second cut. The fructan results of the Rhine samples (second cut) were analysed with a two-way ANOVA for the year 2012. Further, the annual yield was tested with repeated measures ANOVA. In the analysis of the Elbe data set, the experimental predictor variables were precipitation reduction, nitrogen addition, and site. In the analysis of the Rhine data set, the experimental predictor variables were the precipitation treatments (50 % and 25 % precipitation reduction, control with rainout-shelters, and control) and elevation above base flow (high, low). ANOVAs with significant results were followed by Tukey HSD-tests for comparisons between treatment groups. Basic requirements to conduct a parametric ANOVA such as normality and homoscedasticity were visually checked using diagnostic plots. All statistical tests were conducted using STATISTICA 10 (StatSoft Inc.).

Results

Rhine experiment

The annual yield significantly decreased under 50 % precipitation reduction (21.5 ± 2.6 GJ ha^{-1}) compared to the control with rainout-shelters (31.7 ± 3.0 GJ ha^{-1}; Tukey: $p = 0.0248$; repeated measures ANOVA: $F_{3,16} = 4.3$, $p = 0.0215$) and was higher on the wetter (35.2 ± 1.8 GJ ha^{-1}) compared to the dryer site (19.0 ± 0.6 GJ ha^{-1}; Tukey: $p = 0.0002$; repeated measures ANOVA: $F_{1,16} = 52.3$, $p < 0.0001$). When both study years are analysed separately, no differences in annual yield were detected within sites (Tukey: all $p > 0.05$).

Table 4.2: Forage quality parameters of differently treated meadow plots (control, control +shelter), -25 % precipitation, and -50 % precipitation) on the moist and dry meadow site in the floodplain at the Rhine River. The plots were cut in June 2011 and 2012 **(first cuts;** for second cuts of all but ME and NEL see Figs. 2 and 3). Response parameters are biomass (g m^{-2}), XF = crude fibre (% in dw), XP = crude protein (% in dw), DE = digestible energy (MJ kg^{-1} dw), ME = metabolisable energy (MJ kg^{-1} dw), NEL = net energy for lactation (MJ kg^{-1} dw), and Fructan (% in dw); dw = dry weight. Values are means (*x*) + SE; n = 3. The right column indicates differences between moist and dry sites within years. Only P-content differs between treatment groups at the dry site in 2011 (different letters indicating significant differences at p<0.05).

	Moist site								**Dry site**								Significance between sites
	control		control+shelter		-25 %		-50 %		control		control+shelter		-25 %		-50 %		
June 2011	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*p*
Biomass	270.7	22.6	291.6	31.6	233.9	43.0	261.3	54.0	140.5	5.2	147.1	10.0	125.1	6.3	124.0	4.6	0.0003
XF	30.8	0.6	32.4	0.4	33.2	1.3	32.3	<0.1	36.0	0.9	37.1	1.1	36.4	0.3	36.5	0.6	0.0002
XP	9.9	0.5	10.0	1.0	9.1	0.8	8.0	0.4	12.0	0.6	11.4	0.5	11.9	0.7	10.7	1.1	0.0002
DE	8.3	0.1	7.8	<0.1	7.6	0.3	8.0	0.1	6.9	0.2	6.7	0.3	6.8	0.1	6.7	0.2	0.0002
ME	8.4	0.1	7.9	0.2	7.8	0.1	8.2	0.2	7.0	0.2	6.9	0.3	6.8	0.3	6.8	0.5	0.0002
NEL	4.9	0.1	4.5	0.1	4.4	0.1	4.7	0.1	4.0	0.1	3.9	0.2	3.8	0.2	3.8	0.3	0.0002
Fructan	3.2	0.4	2.7	0.3	2.9	0.5	4.3	0.2	0.4	0.1	0.6	0.2	1.4	0.1	1.9	0.3	0.0002
N	12.6	1.0	13.7	1.0	13.2	1.0	11.2	0.7	17.0	0.6	15.6	0.4	16.7	0.5	15.5	1.1	0.0002
P	2.6	0.1	2.6	0.1	2.7	0.1	2.6	0.1	3.8	0.3	3.6	0.1	3.6	0.1	3.1	<0.1	0.0002
K	16.3	0.9	16.0	0.6	16.1	1.7	15.5	0.1	16.8	1.0	17.0	1.1	16.8	0.7	15.7	0.5	0.6897
June 2012																	
Biomass	340.1	33.4	364.2	32.5	324.2	74.6	204.3	54.5	180.1	3.3	215.7	2.1	168.3	17.6	165.9	13.5	0.0003
XF	34.5	0.4	35.6	0.5	35.3	1.1	34.1	0.3	37.1	0.4	39.4	0.4	37.6	0.6	40.4	0.6	0.0002
XP	8.5	0.5	6.9	0.1	7.5	0.7	7.9	0.5	6.2	0.3	5.6	0.2	6.1	0.1	4.8	0.3	0.0004
DE	7.5	0.1	7.3	0.2	7.5	0.2	7.8	0.1	7.2	0.1	6.7	0.1	7.2	0.1	6.6	0.1	0.0003
ME	7.5	0.2	7.6	0.1	7.6	0.2	7.9	0.1	7.6	0.1	7.2	0.1	7.6	0.2	7.1	0.1	0.2144
NEL	4.3	0.1	4.3	0.1	4.3	0.2	4.5	0.1	4.3	0.1	4.1	0.1	4.3	0.1	3.9	0.1	0.1854
Fructan	2.6	0.7	3.0	0.7	4.0	0.5	4.3	0.5	1.8	0.1	0.8	0.2	1.8	0.4	1.4	0.5	0.0002
N	12.9	0.9	11.2	0.4	11.2	1.1	12.4	0.7	10.6	0.4	9.7	<0.1	10.3	0.1	9.0	0.2	0.0021
P	2.6	0.1	2.6	0.1	2.7	0.1	2.8	0.2	4.1 a	0.3	3.8 ab	0.1	3.9 a	0.1	3.0 b	0.1	0.0002
K	16.1	0.4	16.1	0.5	14.5	0.6	14.9	0.6	16.0	0.6	16.0	0.7	15.9	0.5	14.4	0.4	0.9906

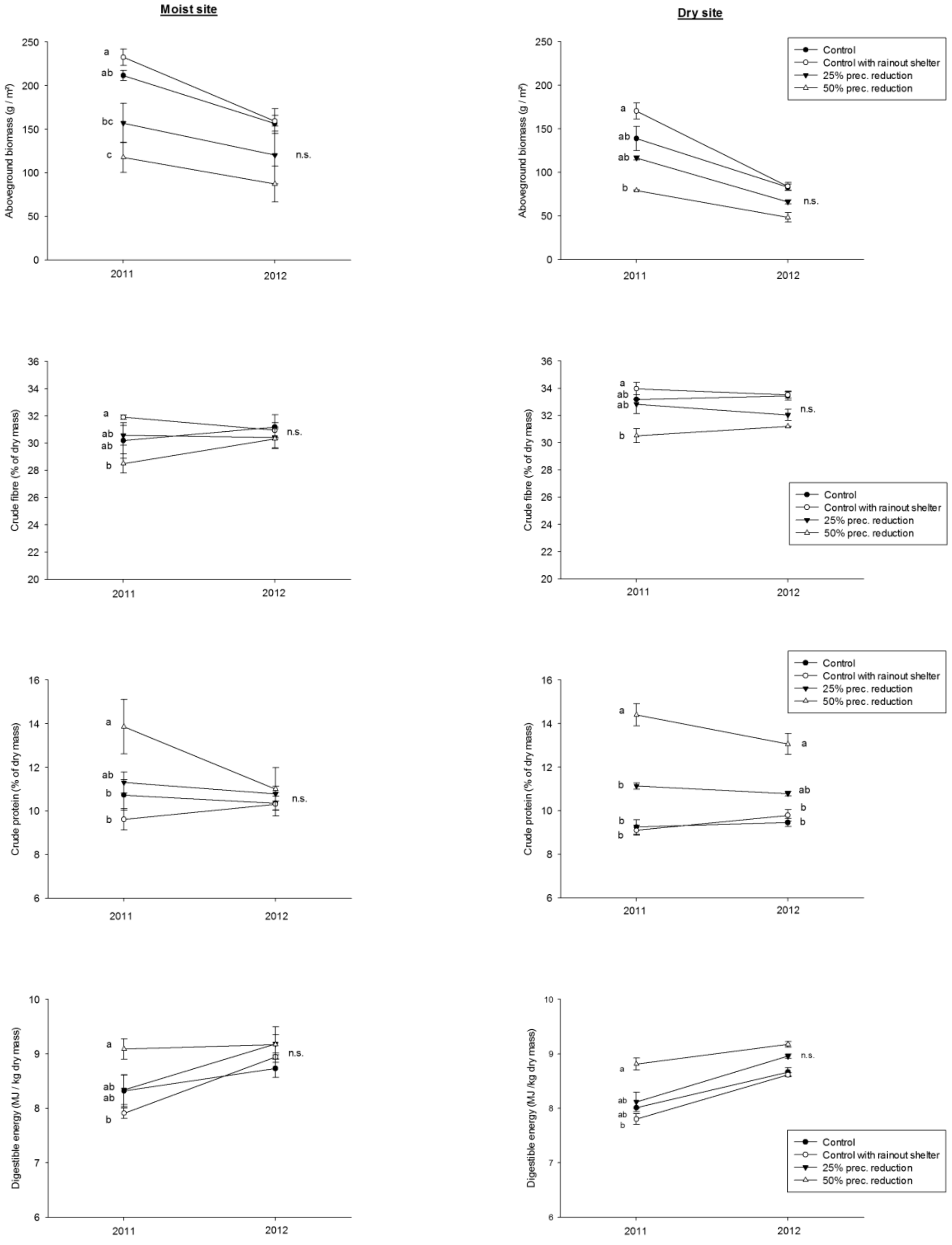

Fig. 4.2: Responses of aboveground biomass and its content of crude fibre, crude protein and digestible energy to experimental treatments. Results refer to autumn cuts of Rhine sites of the years 2011 and 2012. Different letters indicate significant differences at $p<0.05$; (mean ± SE; n = 3).

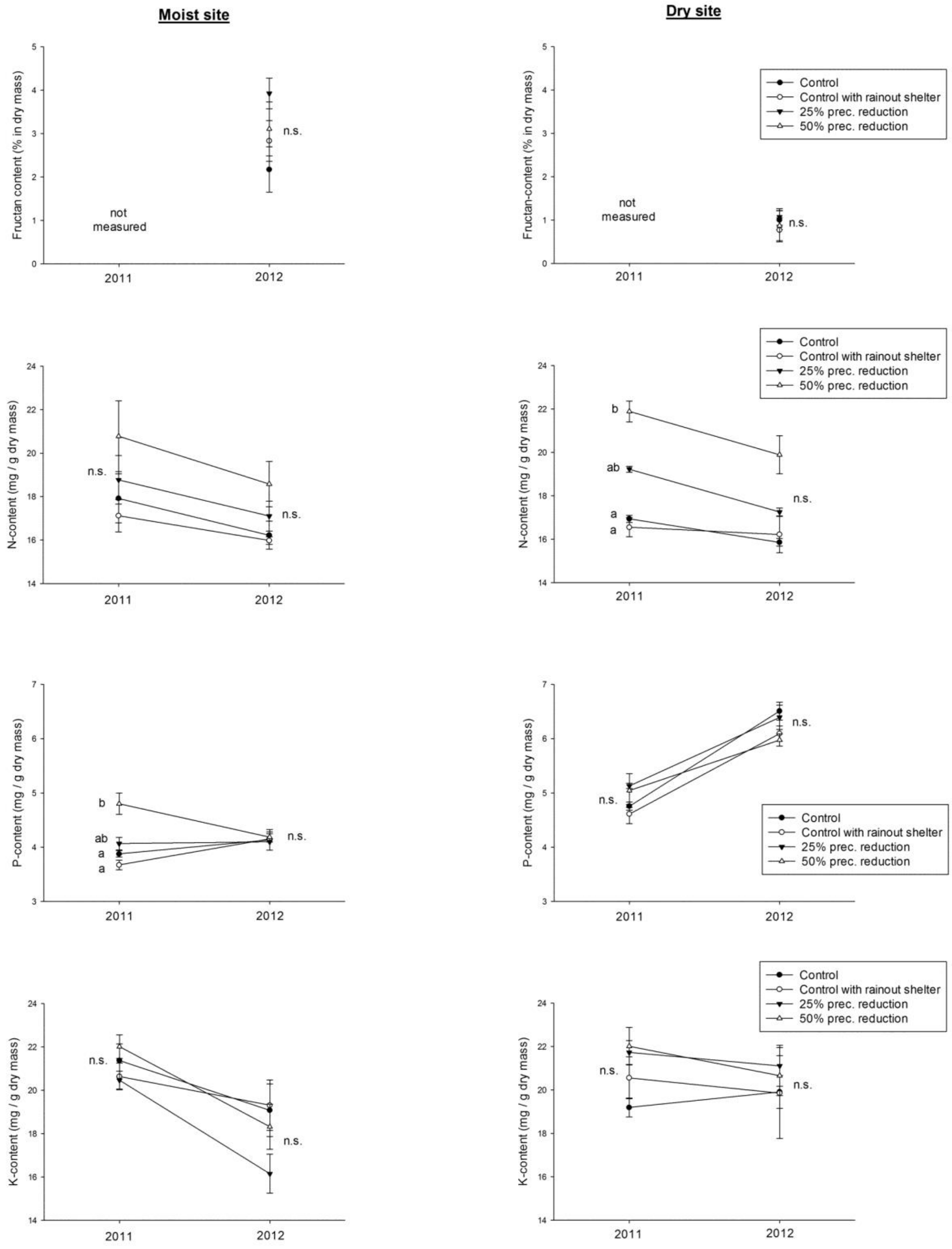

Fig. 4.3: Responses of the content of fructan, N, P, and K to experimental treatments. Results refer to autumn cuts of Rhine-sites of the years 2011 and 2012. Different letters indicate significant differences at $p<0.05$; (Mean ± SE; n = 3).

In the first cut, no main effects of experimental treatments on the amount of biomass (overall mean ± SE: 222.3 ± 13.1 g m^{-2}) or on the forage quality variables crude fibre (35.5 ± 0.4 % dw), crude protein (8.5 ± 0.3 % dw), digestible energy (7.3 ± 0.1 MJ kg^{-1} dw), net energy for lactation (4.2 ± 0.1 MJ kg^{-1} dw), metabolisable energy (7.5 ± 0.1 MJ kg^{-1} dw), and the N- and K-contents (N: 12.7 ± 0.4 mg g^{-1} dw; K: 15.9 ± 0.2 mg g^{-1} dw) were detected. Only the fructan content significantly increased with 50 % reduced precipitation (3.0 ± 0.4 % dw) compared to the controls with rainout shelters (1.8 ± 0.4 % dw; Tukey: $p = 0.0023$) and without rainout shelters (2.0 ± 0.4 % dw; Tukey: $p = 0.0110$; repeated measures ANOVA: $F_{3,16} = 7.9$, $p = 0.0019$), but post-hoc tests were not significant within sites and years. Further, the P-content was significantly affected by precipitation reduction (repeated measures ANOVA: $F_{3,16} = 4.2$, $p = 0.0221$) and by an interaction between 'precipitation reduction' and 'site' (repeated measures ANOVA: $F_{3,16} = 4.7$, $p = 0.0151$). The P-content of the biomass decreased at 50 % precipitation reduction (2.9 ± 0.1 mg g^{-1} dw) compared to the controls without rainout-shelters (3.3 ± 0.2 mg g^{-1} dw; Tukey: $p = 0.0195$) pooled over both sites and both years and also, the P-content differed between differently treated groups at the dryer site in 2012 (see Table 4.2).

In the second cut, all response variables (except for K-content and fructan) were affected by the precipitation treatments (Figs. 4.2 and 4.3). The two differently elevated sites mainly reacted in the same way – an interaction between precipitation reduction and elevation was only detected for the response variable P-content (repeated measures ANOVA: $F_{3,16} = 3.6$, $p = 0.0365$). At both elevations, crude fibre and biomass decreased under precipitation reduction treatments while crude protein and digestible energy increased in 2011. In 2012, the effects of precipitation treatments were generally less pronounced and only crude protein contents differed significantly at the dryer site between plots with 50 % precipitation reduction and controls with rainout-shelters (see Fig. 4.2).

Elbe experiment

The annual yield did not respond significantly to the precipitation reduction of 25 % (repeated measures ANOVA, $F_{1,48} = 0.4$, $p = 0.51$). A significant interaction between 'precipitation reduction', 'N-addition', 'year', and 'site' (repeated measures ANOVA, $F_{1,48} = 4.8$, $p = 0.0328$) did not lead to significant differences between treatment groups within years and sites. In the study years 2010 and 2011, annual yields were significantly higher (repeated measures ANOVA, $F_{1,48} = 45.9$, $p < 0.0001$) at the more continental site (2010: 57.8 ± 1.8 GJ ha^{-1}; 2011: 63.1 ± 1.5 GJ ha^{-1}) than at the oceanic site (2010: 48.5 ± 2.2 GJ ha^{-1}; 2011: 40.2 ± 1.7 GJ ha^{-1}).

In the first cut of the experimental grasslands in the Elbe region, no main effects of the experimental treatments were detected on any of the response variables (for mean values of the variables see Appendix 4.1). However, significant differences occurred between the two sites characterised by different climatic conditions (for *p*-values between sites within years see Appendix 4.1). Significant interactive effects of 'precipitation reduction' and 'site' on crude protein (repeated measures ANOVA, $F_{1,48} = 5.2$, $p = 0.0264$) and N-content (repeated measures ANOVA, $F_{1,48} = 6.8$, $p = 0.0120$) indicated that these variables were not affected by precipitation reduction at the oceanic site (mean over both years ± SE: crude protein: 11.2 ± 0.3 % dw, N: 19.6 ± 0.4 mg g^{-1} dw under reduced precipitation compared to crude protein: 10.9 ± 0.3 % dw and N: 18.4 ± 0.4 mg g^{-1} dw in control plots), while they tended to decrease under reduced precipitation at the more continental site (crude protein: 10.7 ± 0.2 % dw, N: 17.3 ± 0.3 mg g^{-1} dw under reduced precipitation compared to crude protein: 11.9 ± 0.4 % dw, N: 18.4 ± 0.5 mg g^{-1} dw in control plots). Further, the differences between years 2010 and 2011 were significant for all response variables (all $p < 0.0001$) except for fructan ($F_{1,48} = 0.7$, $p = 0.3938$).

In the second cut, the quantity and quality of the biomass did not respond to main effects of the experimental treatments. As in the first cut, main effects were only detected between the two sites with differing climatic conditions (for p-values between sites within years see Appendix 1). Further, the differences between years (2009 – 2011) were significant for all response variables (repeated measures ANOVAs, all $p < 0.0001$) except for fructan ($F_{2,96} = 2.5$, $p = 0.0878$). Though not significantly, the percentage of crude fibre tended to decrease under precipitation reduction at the oceanic site, and tended to increase under these conditions at the more continental site (repeated measures ANOVA, $F_{1,48} = 2.9$, $p = 0.0941$). *Vice versa*, the amount of digestible energy tended to increase under precipitation reduction at the oceanic site, while it tended to decrease under these conditions at the more continental site (repeated measures ANOVA, $F_{1,48} = 3.2$, $p = 0.0797$).

Discussion

Forage quality of floodplain meadows

The productivity of the meadows in this study is in the same range as of other flood meadows (Franke 2003, Donath et al. 2004), but lower than that of non-flooded meadows (Walter et al. 2012) or fertilized semi-natural grasslands (Tallowin and Jefferson 1999). Generally, data on crude fibre, crude protein, energy content and fructan of European semi-natural grasslands are scarce in the literature. The few existing studies report values of these variables in the range of our study (Franke 2003, Donath et al. 2004). Our contents of N, P and K were very variable, but roughly in the same range (Olde Venterink et al. 2006) or lower (Tallowin and Jefferson 1999) compared to other studies on semi-natural grasslands. The hay quality of semi-natural floodplain meadows is low compared to agriculturally improved and intensively used sown hay meadows (Tallowin and Jefferson 1999). This is in accordance with Franke (2003) who concluded that the hay originating from semi-natural meadows is especially suitable for leisure horses and young cattle or not lactating cows. For lactating cows, the energy content is too low (Franke 2003) but can be incorporated into basic ration (NRC 2001).

Rhine experiments

Overall, the annual yield decreased under precipitation reduction in the experiment at the Rhine River. The higher forage quality in the second cut did not compensate for the lower harvested amount of biomass at reduced precipitation conditions. Therefore, our findings indicate that climate change will affect the quantity and quality of hay in the future.

The responses of the meadow vegetation to the experimental treatments were more pronounced in the second than in the first cut. Most importantly, the amount of biomass and its content of crude fibre decreased under reduced precipitation in the second cut, while interestingly, the digestible energy and the contents of crude protein, N, and P increased in the biomass. Generally, an increase in hay quality in dry years was already reported by Opitz von Boberfeld (1994) but the underlying processes still remain unclear. The N-contents in the biomass might have been higher at the precipitation reduction treatment because of slower re-growth of the meadow plants after the first cut. Under dryer conditions, plant development is decelerated (Hsiao and Acevedo 1974) and the aboveground biomass remains longer in an earlier phenological state, i.e. it consists mainly of leaves at harvest compared to plots with full precipitation, where plants already developed stems. The N concentration in leaves is greater than in stems and the nitrogen concentration of the whole herbage depends largely on the leaf/stem ratio (Duru et al. 1997). Another explanation for the higher N- and protein contents under reduced precipitation might be found in an enhanced variability in soil moisture. Fluctuations in moisture content stimulate nutrient mineralisation (Bloor and Bardgett 2012). Especially the extractable P pool was reported to increase upon soil re-wetting (Olde Venterink et al. 2002). These fluctuations may be the reason why we detected higher P-contents in the biomass of the control plots in spring 2012 on the dry site while on the contrary we measured higher P-values under experimentally reduced precipitation in the plant foliage in autumn 2011 on the wetter site. Drought stress also increased foliar N and P concentration of eastern cottonwood *Populus deltoides* (Broadfoot and Farmer 1969) and in *Salix* spp. (Weih et al. 2011). The observation that plants absorb nutrients at a higher rate than is required for their actual plant growth when another resource is limiting is interpreted as advantageous as these absorbed nutrients can be readily incorporated in assimilates when the limiting resource is available again (Chapin 1980). Further, higher concentration of osmotic compounds (e.g. N containing amino-acids) allows the plants to better gain soil water (Morgan 1984). Enriched osmotic compounds in the plants decrease the water potential of the plants (which becomes more negative) and plants thus increase their ability to take up water from relatively dry soils.

Elbe experiments

The precipitation reduction of 25 % did not affect the quantity and quality of hay from the meadows at the Elbe tributaries (as this was also the case under the 25 % treatment at the Rhine River). The nitrogen input of 35 kg ha^{-1} a^{-1} had also no effect and was probably negligible compared to inputs by flooding events, which are the main source of nutrients in floodplain ecosystems (e.g. Beltman et al. 2007). Besides of the weak treatment effects, our data demonstrate a high variability of the response variables between the study years. This is probably due to the differing weather conditions of the study years. Shortly before the second cuts, the weather conditions were very dry in 2009, very wet in 2010, and intermediate in 2011 (see Fig. 4.1a and 4.1b). High variability of the response variables was also found between the sites along the climatic gradient.

It is striking that the responses of crude fibre and energy content were completely different between the two Elbe sites. A possible explanation for the different findings at the two Elbe sites could be that the percentage of dicots differed between the sites. The oceanic site (with the tendency of reduced crude fibre and higher energy at reduced precipitation in the second cut) showed higher abundances of grasses compared to the more continental site, which tended to develop reduced energy and higher crude fibre in the second cut hay at reduced precipitation (see Fig. 4.S1). The grasses mostly reproduce (i.e. set seeds) before the first cut in floodplain grasslands and grow leaves until the second cut. As mentioned above, the N concentration (and energy content) is larger in leaves than in stems (Duru et al. 1997). Accordingly, leaves are less rich in crude fibre. In the more continental site, the dicots might have been in the process of reproduction at the second cut, in which the reduced precipitation might have had a ‘slow down’ effect on the reproduction process.

Overall, the meadows at the Rhine were more responsive to the experimental treatments than the Elbe meadows. This may, on the one hand, be due the lack of a -50 % reduction treatment in the Elbe experiment. Therefore, the measured responses were limited and the effects at the Elbe River may be underestimated. On the other hand, the ‘new’ meadows of the Rhine floodplain were less species rich compared to the ‘old’ meadows at the Elbe tributaries. Species richness might have buffered possible effects of reduced precipitation on the response variables. In species-rich stands, some species may be facilitated through the treatments, compensating reduced growth of other species and thus increasing the reliability of grassland productivity under variable conditions (Tilman and Downing 1994, Chapin et al. 2000). The role of meadow age and species richness in the drought resilience of grasslands requires further research.

Conclusions

The annual yield decreased under precipitation reduction of 50 % in the experiment at the Rhine River. Therefore, we conclude that the yield of floodplain meadows may become less reliable in future. Nevertheless, the effects of the two precipitation reduction experiments on forage quality and the amount of biomass were, overall, rather small. This finding fits with other studies reporting weak or no effects of drought events on grassland productivity (Kreyling et al. 2008, Bloor et al. 2010, Jentsch et al. 2011, Walter et al. 2012). The first cut was not affected by precipitation reduction (except for fructan at the Rhine sites) in the floodplain meadows at both rivers. As the first cut is more important for agricultural purposes, at least the use of the first cut hay may be possible under climate change. In case of our studied floodplain meadows, soil moisture was probably sufficient for plant growth from winter/spring until the first cut in June. It has to be considered that the groundwater levels of floodplains correspond to the water level of the associated river.

Consequently, whether the productivity of the floodplain meadows will be affected in future will largely depend on whether the river discharges will decrease during winter and spring in future. Finally, multiple factors change simultaneously in the course of climate change. Additive effects of reduced summer precipitation, higher temperatures and increased CO_2 concentrations, and possibly lowered groundwater tables are possible.

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Supplementary Material

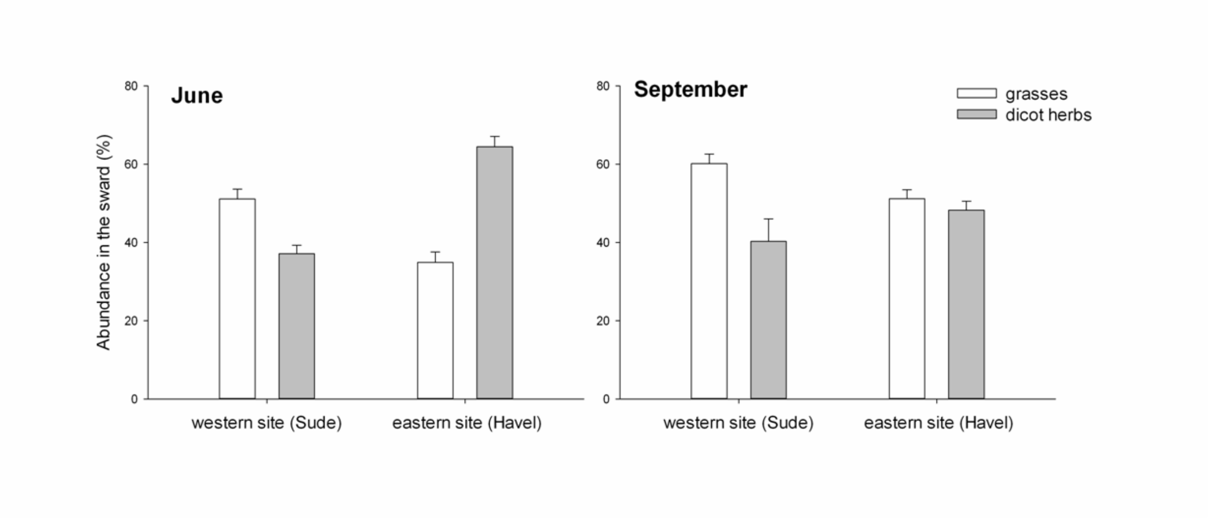

Fig. 4.S1: The abundance of the functional groups grasses and herbs at the time of cutting in June and September 2011 at the experimental sites at the Elbe tributaries Sude and Havel.

Appendix

Appendix 4.1: Forage quality parameters of differently treated meadow plots (control, +N, -25 %, and +N/-25 %) at the Elbe River (oceanic site at the Sude and more continental site at the Havel River). The plots were cut in June 2010 and 2011 **(first cuts)** and in September 2009, 2010 and 2011 **(second cuts)**. Response parameters are biomass (g m^{-2}), XF = crude fibre (% in dw), XP = crude protein (% in dw), DE = digestible energy (MJ kg^{-1} dw), ME = metabolisable energy (MJ kg^{-1} dw), NEL = net energy for lactation (MJ kg^{-1} dw), Fructan (% in dw), and annual yield (GJ ha^{-1}); dw = dry weight. Values are means (*x*) + SE. n = 7 for all groups. No differences were detected between treatments within sites and years, only between sites (right column).

Sep. 2009	**Sude (oceanic site)**								**Havel (more continental site)**								Significance between sites
	control		+N		-25 %		+N/-25 %		control		+N		-25 %		+N/-25 %		
	x	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*p*
Biomass	197.9	11.0	200.2	13.8	192.6	10.2	217.5	15.8	211.6	16.4	211.0	9.7	190.4	12.8	199.0	13.5	1.0000
XF	30.4	0.4	28.7	0.5	29.1	0.4	29.2	0.5	27.1	0.7	26.9	0.6	28.2	0.6	27.1	0.6	0.0011
XP	10.7	0.4	10.9	0.3	10.3	0.5	10.9	0.4	10.2	0.6	11.1	0.5	10.4	0.5	10.3	0.4	0.9962
DE	8.0	0.1	8.4	0.1	8.3	0.2	8.3	0.1	8.9	0.2	8.9	0.2	8.7	0.2	8.9	0.2	<0.0001
ME	7.6	0.1	7.8	0.1	7.9	0.2	8.0	0.1	8.2	0.2	8.2	0.2	8.0	0.2	8.3	0.2	0.0302
NEL	4.3	0.1	4.5	0.1	4.5	0.1	4.6	0.1	4.7	0.1	4.7	0.1	4.6	0.1	4.8	0.1	0.0307
Fructan	0.4	0.2	0.7	0.3	1.3	0.6	0.9	0.7	1.7	0.4	1.4	0.4	2.9	0.5	2.7	0.3	0.0088
N	17.6	0.5	17.9	0.3	17.3	0.7	18.1	0.6	16.2	0.9	17.5	0.6	16.2	0.8	16.2	0.6	0.0855
P	1.8	0.2	1.7	0.1	1.9	0.2	1.9	0.3	2.9	0.2	2.7	0.1	2.8	0.2	2.9	0.2	0.0001
K	7.2	0.4	6.8	0.2	7.8	0.2	8.8	0.2	7.0	0.5	6.8	0.3	6.8	0.3	6.6	0.4	0.0546

Appendix 4.1 (continued):

	Sude (oceanic site)								**Havel (more continental site)**								Significance between sites
	control		+N		-25 %		+N/-25 %		control		+N		-25 %		+N/-25 %		
June 2010	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*p*
Biomass	363.4	52.5	392.3	49.0	381.5	37.2	445.1	32.4	360.4	25.0	405.2	20.2	427.9	28.6	429.8	26.5	0.9689
XF	30.2	0.7	29.9	1.1	30.6	0.7	30.5	0.5	28.1	0.9	29.5	0.8	32.0	0.6	29.6	0.8	0.8640
XP	10.2	0.5	9.7	0.4	10.4	0.6	10.3	0.2	12.5	1.0	11.6	0.7	10.2	0.4	10.5	0.5	0.0381
DE	8.3	0.1	8.4	0.2	8.3	0.2	8.3	0.1	8.8	0.2	8.5	0.2	8.1	0.2	8.6	0.1	0.4694
ME	8.3	0.2	8.5	0.1	8.5	0.1	8.5	0.1	8.9	0.2	8.7	0.2	8.4	0.1	8.8	0.1	0.0684
NEL	4.8	0.1	4.9	0.1	4.9	0.1	4.9	0.1	5.2	0.1	5.0	0.1	4.9	0.1	5.1	0.1	0.0685
Fructan	3.0	0.8	3.8	0.9	3.2	0.7	2.6	0.5	2.6	0.8	2.6	0.6	3.4	0.6	3.2	0.8	0.9747
N	16.5	0.4	16.6	0.5	17.6	0.5	18.3	0.8	19.1	1.5	17.1	0.5	17.2	0.6	16.4	0.6	0.9812
P	2.0	0.1	2.0	0.1	2.3	0.1	2.1	0.1	3.3	0.2	2.9	0.1	3.0	0.2	3.1	0.2	0.0002
K	10.5	0.3	10.0	0.3	11.3	0.6	11.1	0.5	13.8	1.0	13.2	0.8	14.0	0.8	13.6	1.0	0.0002
Sep. 2010																	
Biomass	174.0	25.1	162.9	13.1	174.1	21.2	193.2	9.0	231.0	24.6	264.4	19.1	252.1	19.2	251.8	27.1	0.0001
XF	26.2	0.8	26.3	1.2	24.9	0.5	26.5	0.7	24.1	0.8	25.5	0.6	25.9	0.7	25.1	0.5	0.5913
XP	14.1	0.5	13.5	0.5	14.0	0.5	14.1	0.7	13.7	0.6	13.6	0.7	13.2	0.4	13.7	0.4	0.9088
DE	8.8	0.2	8.8	0.3	9.1	0.2	8.9	0.1	9.6	0.2	9.3	0.2	9.2	0.2	9.3	0.2	0.0027
ME	8.5	0.2	8.4	0.2	8.6	0.2	8.6	0.1	9.2	0.2	9.0	0.2	9.0	0.2	9.1	0.2	<0.0001
NEL	4.9	0.1	4.9	0.1	5.0	0.1	5.0	0.1	5.4	0.1	5.3	0.2	5.2	0.1	5.4	0.1	<0.0001
Fructan	0.5	0.5	1.1	0.5	0.2	0.2	0.6	0.5	1.2	0.3	1.7	0.7	2.3	1.0	1.1	0.5	0.1856
N	22.5	0.7	22.5	0.8	22.9	0.7	23.4	0.6	21.4	0.9	21.3	0.9	21.0	0.4	20.6	0.3	0.0029
P	2.3	0.1	2.3	0.1	2.7	0.2	2.4	0.2	3.7	0.2	3.5	0.3	3.5	0.2	3.4	0.3	0.0001
K	11.1	0.4	9.5	0.4	10.6	0.3	10.4	0.2	11.4	0.6	11.5	0.8	11.1	0.5	11.0	0.6	0.0781
Overall yield 2010	45.3	6.0	46.8	4.1	47.5	4.4	54.5	2.8	43.4	4.3	58.8	1.9	50.4	4.1	60.1	4.3	0.0046

Appendix 4.1 (continued):

	Sude (oceanic site)								**Havel (more continental site)**								Significance between sites
	control		+N		-25 %		+N/-25 %		control		+N		-25 %		+N/-25 %		
June 2011	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*x*	SE	*p*
Biomass	194.8	26.7	227.2	35.1	199.8	19.0	204.1	29.1	383.4	33.0	340.4	32.7	372.2	21.6	372.5	19.6	0.0002
XF	27.5	1.1	27.5	1.2	26.8	1.2	27.4	1.0	25.6	0.6	24.8	0.8	26.9	0.7	25.8	0.7	0.0594
XP	11.7	0.4	12.0	0.5	11.5	0.3	12.6	0.7	11.6	0.7	11.9	0.6	10.9	0.3	11.1	0.6	0.4492
DE	8.7	0.2	8.7	0.2	8.9	0.2	8.7	0.2	9.1	0.1	9.3	0.2	8.8	0.1	9.1	0.1	0.0720
ME	8.6	0.2	8.6	0.2	8.7	0.2	8.6	0.2	9.1	0.1	9.2	0.1	8.9	0.1	9.1	0.1	0.0014
NEL	5.0	0.1	5.0	0.1	5.1	0.1	5.0	0.1	5.3	0.1	5.4	0.1	5.2	0.1	5.3	0.1	0.0011
Fructan	1.5	0.4	2.0	0.5	1.6	0.6	0.7	0.2	3.7	0.9	4.4	0.6	4.4	0.6	4.3	0.6	0.0002
N	19.8	0.7	20.5	0.5	21.5	0.6	20.9	0.4	19.1	1.1	18.3	0.6	17.3	0.4	18.1	0.6	0.0002
P	1.9	0.1	2.0	0.1	2.2	0.1	2.0	0.2	2.8	0.1	2.6	0.1	2.5	0.1	2.5	0.1	0.0002
K	10.7	0.4	9.4	0.6	10.1	0.7	9.8	0.6	11.7	0.5	12.0	0.7	11.6	0.7	11.4	0.6	0.0032
Sep. 2011																	
Biomass	245.7	13.1	289.1	31.6	270.5	29.8	269.3	17.9	343.3	20.9	354.4	18.7	326.3	21.0	345.2	13.0	0.0001
XF	26.4	1.0	27.7	0.7	25.9	0.9	27.9	0.9	24.2	0.8	25.4	0.5	26.0	0.3	26.1	0.6	0.0273
XP	12.9	0.7	13.4	0.9	12.9	0.5	13.9	0.7	12.7	0.6	12.5	0.3	12.2	0.7	12.5	0.8	0.3485
DE	8.4	0.2	8.2	0.2	8.5	0.1	8.2	0.2	9.0	0.1	8.7	0.1	8.7	0.1	8.7	0.1	0.0016
ME	8.2	0.1	8.0	0.1	8.1	0.1	8.0	0.2	8.7	0.1	8.5	0.1	8.5	0.1	8.5	0.1	0.0004
NEL	4.7	<0.1	4.5	0.1	4.7	0.1	4.6	0.1	5.1	0.1	5.0	<0.1	5.0	0.1	5.0	0.1	0.0003
Fructan	0.8	0.3	1.7	1.0	1.0	0.5	1.5	0.6	1.7	0.7	1.7	0.5	2.4	0.8	1.8	0.7	0.6503
N	21.2	0.5	22.2	0.8	21.2	0.6	22.8	0.6	19.5	0.6	19.2	0.3	18.8	0.5	19.0	0.7	0.0001
P	2.8	0.2	3.2	0.2	3.2	0.2	3.5	0.3	3.6	0.2	3.4	0.2	3.3	0.3	3.3	0.2	0.6205
K	8.6	0.5	7.7	0.2	8.1	0.5	8.3	0.3	11.5	0.7	11.3	0.4	11.4	0.6	11.2	0.6	<0.0001
Overall yield 2011	37.3	2.8	43.0	4.3	40.7	3.1	39.8	3.5	65.4	3.4	62.4	3.5	61.1	3.3	63.7	2.4	0.0002

CHAPTER 5

EFFECTS OF WATER LEVEL AND COMPETITION ON THE ENDANGERED RIVER CORRIDOR PLANT *CNIDIUM DUBIUM* IN THE CONTEXT OF CLIMATE CHANGE

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Abstract

River corridors are hotspots of biodiversity and harbour plant species which are predominantly distributed in this dynamic ecosystem (river corridor plants). During the last centuries, floodplain meadows became increasingly threatened due to dike constructions and land use changes. An additional threat from future climate change might be posed by the increased probability of drought during summer due to reduced precipitation and water levels in the rivers. Our aim was to test how the characteristic floodplain meadow plant *Cnidium dubium* responds to water level changes, and to develop implications for its management in the course of climate change.

Two mesocosm experiments were set up with plants originating from floodplain meadows along two tributaries of the Elbe River, Germany. In the first experiment, we investigated growth characteristics and biomass of juvenile *C. dubium* individuals in response to groundwater level (20, 40, and 60 cm below soil surface) and origin. In the second experiment, competitors were included to analyse interactive effects of competition and the water level on mature plants of *C. dubium*.

The growth of *C. dubium* was affected by the water level, with a physiological optimum at water levels of 40 – 60 cm below soil surface. *C. dubium* showed adaptations to the sites of seed origin and evidence for phenotypic plasticity in relation to competition, which suggests that this species might possess adaptation potential. Nevertheless, we propose raising the groundwater level to 20 – 60 cm below soil surface as a possible management strategy, when drought (as a consequence of climate change) is perceivable.

Keywords

Alluvial * competition * drought stress * groundwater level * local adaptations * phenotypic plasticity

Introduction

River corridors are known to be hotspots of biodiversity (Naiman et al. 1993, Tockner and Stanford 2002). The distribution of some plant species – the so-called river corridor plants – is closely bound to these ecosystems (Burkart 2001). The high diversity of river corridors is a result of the dynamic environmental conditions of the floodplains. In semi-natural grasslands of the floodplains along rivers of Europe, the dynamic hydrological conditions lead to complex mosaics of plant communities on small scales (Joyce and Wade 1998). The floodplain meadows under low-intensity land use (mown once or twice annually) are particularly species rich (Härdtle et al. 2006, Gerard et al. 2008), and those belonging to the alliance Cnidion dubii are protected in Europe under the Habitats Directive (92/43/EEC, habitat type 6440).

Floodplains are termed 'functional' as long as they are directly connected to the corresponding river and thus are flooded frequently by river water during high water levels (*sensu* Leyer 2004). Therefore, the dynamic hydrological conditions prevail in these ecosystems, which are needed for the occurrence of river corridor species (Burkart 2001). In recent centuries, functional floodplains decreased dramatically in Europe due to straightening and canalisation of rivers and dike construction (Tockner and Stanford 2002; Brunotte et al. 2009; Čížková et al. 2013). By way of example, the flooding area along the Middle Elbe River declined by 50-90 % (Brunotte et al. 2009). Changes in land use have additionally contributed to the decline of species-rich floodplain grasslands during the last decades (Wesche et al. 2012). In the future, the threats to these ecosystems may increase due to climate change (see Erwin 2009; Čížková et al. 2013).

Climate models for Central Europe predict more intense precipitation events, but occurring less frequently, leading to prolonged drought phases between single precipitation events (IPCC 2007; Görgen et al. 2010). This induces a higher risk of reduced soil water content, especially if surface runoff increases (Knapp et al. 2008). On a regional scale, climate change modelling for northern Germany projects a decline of 20 – 30% in summer precipitation by the end of this century (Jacob et al. 2008). In addition, the altered climate might lead to reduced water levels in rivers, especially during summer (Conradt et al. 2012). This would consequently lower the groundwater table in the adjacent floodplains. In combination with increased transpiration at higher temperatures, these changes could induce drought stress for the plants of floodplain meadows (Jensen et al. 2011).

The consequences of climate change on the vegetation of floodplain meadows and on river corridor plants are still poorly understood. One way species might react to climate change would be long-distance migration by dispersal to new sites that are climatically better suited for growth and reproduction. There is evidence, however, that many plant species are not able to migrate fast enough to new potential habitats (Honnay et al. 2002; Higgins et al. 2003). In particular for rare and endangered species with small population sizes, successful migration through the highly fragmented landscape of Europe seems to be rather unlikely (Donath et al. 2003). Thus, the other option for persistence in a changing environment would be adaptation (Berg et al. 2010). In general, the adaptation potential of a plant species is affected by genetic variation and by phenotypic plasticity (Pauls et al. 2012).

If the adaptation potential of floodplain meadow plants turns out to be insufficient under climate change, a management strategy for this ecosystem would be necessary. Therefore, it is crucial to understand the interactions of the rare species with their abiotic and biotic environment. Most important in floodplains are the hydrologic conditions (Toth and van der Valk 2012), ranging from moist conditions at lower to dry conditions at higher elevations. The species usually have a specific physiological optimum in relation to the hydrological regime (Silvertown *et al.* 1999; van Eck *et al.* 2004). The biotic plant – plant interaction 'competition' is another important factor shaping plant communities in floodplains (Ellenberg 1954, Grime 1979). Under competition, some species shift their occurrence along hydrological gradients away from their physiological optimum to conditions where competition is lower (ecological optimum *sensu* Ellenberg 1954).

We conducted experiments with the endangered river corridor plant *Cnidium dubium* (Ludwig and Schnittler 1996), which is characteristic for species-rich floodplain meadows under hydrologically dynamic conditions (Leyer 2002; Härdtle et al. 2006) and considered to be a weak competitor (Härdtle et al. 2006).

The aim of this study was to test how the performance of *C. dubium* is related to water level and competition. Furthermore, we want to derive implications for the management of floodplain meadows in the course of climate change. In the first experiment, carried out with juveniles of *Cnidium dubium* that were raised as seedlings under equal conditions, we investigated the effects of origin and water levels on *Cnidium dubium* (the experiment without competition). In the second experiment, carried out with adult plants in sods, we assessed the role of water level under the presence of naturally co-occurring competitors (the sod experiment). We addressed the following research questions: 1.) At which water level does *C. dubium* perform best without competing plants? 2.) How do the different water levels influence the growth of *C. dubium* under competition? 3.) Do the juveniles grown from seeds of different origins differ in their growth and in response to the applied water levels?

Materials and methods

Study species

C. dubium is a small rosette-forming, biennial to perennial herb from the Apiaceae family (Hegi 1965). It develops vegetative shoots resulting in new plants (Asby 1973; Geißler and Gzik 2008b). One genet, therefore, consists of many clonal ramets.

Sites of seed and sod origin

Two areas of floodplain meadows in the UNESCO Biosphere Reserve Elbe River Landscape in Germany were selected as sources for seeds of *C. dubium* and sods of floodplain meadows. One area is located under rather oceanic climatic conditions along the Sude River near Sückau (N53°19.137 E010°57.290). It is characterized by a mean annual precipitation of 663 mm and a mean annual temperature of 8.3 °C (1961 – 1990; data from the nearest weather station in Boizenburg; DWD). The other area is located under more continental climatic conditions along the Havel River near Kuhlhausen (N52°47.037 E012°11.665). In this area, the mean annual precipitation is 503 mm (1961 – 1990; data from the nearest weather station in Havelberg; DWD) and thus, is ca 25 % lower than at the Sude River. The mean annual temperature is 9.1 °C (1976 – 2009; data from the nearest weather station measuring temperature in Seehausen; DWD).

In order to relate our experimental water levels to the hydrological conditions at the study sites, groundwater gauges (Cera-Diver and CTD-Diver, Schlumberger Water Services, Delft, Netherlands) were installed at two (in 2010) and three (in 2011) floodplain meadows during the hydrological summers (see Table 5.1). Water levels were logged at 30 min intervals. Mean water levels of the hydrological summers were calculated for each gauge. The groundwater levels of the two sites of seed and sod origin at the Havel and Sude River were in the same range, on average 48 cm (Havel) and 45.8 cm (Sude) below soil surface. The groundwater levels we measured in the meadows indicate that the artificial water levels of our experiments lay in a realistic range, and are comparable to other floodplain meadows (Gerard et al. 2008).

Table 5.1 Groundwater levels (WL) (mean ± SD, minimum and maximum cm below soil surface) and number of days of inundation in summer 2010 and 2011 (May - October; only Sude 2: August - October), measured at three of the floodplain meadows, which were the sites for seed and sod origin.

	2010		**2011**			**Mean**		
	Havel	Sude	Havel	Sude	Sude 2	Havel	Sude	Both
WL Mean	30.3	50.2	65.7	42.8	42.6	48.0	45.8	46.3
WL SD	35.0	45.3	14.5	35.2	10.9	32.1	36.9	28.2
WL Min	-72.4	-34.4	27.2	-30.8	1.5	-72.4	-34.4	-21.8
WL Max	122.7	126.5	95.6	96.9	73.7	122.7	126.5	103.1
Days of inundation	28	21	0	26	0			

Negative values of groundwater levels refer to flooded conditions

The functional floodplains along the Sude and Havel are typically used as grasslands. Wet and mesic meadows are tightly intermingled on small scales. Some of the grasslands are used for grazing of livestock, and some are mown twice a year. We selected ten grassland sites of 0.1 – 0.3 ha size, with similar vegetation composition with relatively high abundances of *C. dubium* (five at each area, Sude and Havel River). Most sites are regularly mown twice a year, but two grasslands at the Sude were not mown but grazed. All sampled grasslands are regularly flooded by the Sude or the Havel River. Besides river corridor plants like *C.dubium* (Sude and Havel: app. 11 % vegetation cover on 25 m² vegetation records), *Stellaria palustris* (Sude: 1.5 %; Havel: 0.5 %) and *Carex praecox* (Sude: 0.5 %; Havel: 3.5 %), frequently occurring species of our study sites are *Alopecurus pratensis* (Sude: 29 %; Havel: 15 %), *Deschampsia cespitosa* (Sude: 5 %; Havel: 2 %), *Phalaris arundinacea* (Sude: 6 %; Havel: 13 %), *Poa pratensis* (Sude: 11 %; Havel: 26 %), *Poa trivialis* (Sude: 3 %; Havel: 6 %), *Potentilla anserina* (Sude: 5 %; Havel: 2 %), *Ranunculus repens* (Sude: 6 %; Havel: 8 %) and *Vicia cracca* (Sude: 3 %; Havel: 4 %). Nomenclature of plant species follows Wisskirchen and Haeupler (1998).

Seeds of *C. dubium* were collected in October 2009 for the experiment without competition, conducted in 2010. In each area, the seeds were collected from three populations and within each population from at least 10 individuals. In May 2011, 60 sods of floodplain meadows (diameter: 15 cm, depth: 20 cm) were cut out of the meadows for the sod experiment and transported to Hamburg, where the experiment took place. Each sod contained at least one ramet of *C. dubium* and its co-occurring competitors. On average, each sod included eight plant species. In total, 51 plant species were found in all sods, of which the most frequent were *Alopecurus pratensis* (occurring in 66 % of the sods), *Poa pratensis* (50 %), *Potentilla reptans* (48 %), *Vicia cracca* (28 %), *Glechoma hederacea* (27 %), *Ranunculus repens* (24 %), *Phalaris arundinacea* (22 %) *Potentilla anserina* (20 %), *Elymus repens* (18 %), *Poa trivialis* (18 %), and *Lathyrus pratensis* (17 %).

Design and setup of experiments

For the experiment without competition, the seeds of *C. dubium* were stored in dry and dark conditions until the beginning of January 2010. From January 2010 onwards, the seeds were cold-wet stratified for 14 weeks. Afterwards, all seeds were treated with gibberellic acid (5 mM) to increase germination potential. Germination took place in climate chambers at 20 °C during day (12 h light) and 10 °C during nights (12 h dark). 120 seedlings were grown in small pots until June 2010 and were then transplanted into 1-m high pots, which were filled with a substrate mixture of standard garden soil (Floraton 3 by Floragard GmbH: Oldenburg, Germany) and sand. As *C. dubium* plants were grown without competing plants, we refer to this experiment as the "experiment without competition". The 1-m high pots were randomly distributed onto three different levels in two water basins (in the common garden of the Biocenter Klein Flottbek; Hamburg, Germany) to simulate groundwater levels of 20, 40 and 60 cm below soil surface. As the water basins were placed outdoor, the pots were exposed to the natural rainfall (precipitation pattern: Fig. 5.1). In order to keep the water levels of the experiment constant, water was refilled in the water basins when it was lost due to evaporation, and drained when the water levels were too high due to precipitation events. In the experiment without competition, the pots measured 10 cm in diameter, resulting in 20 replicates per water level and origin. The experiment without competition was conducted from July to October 2010.

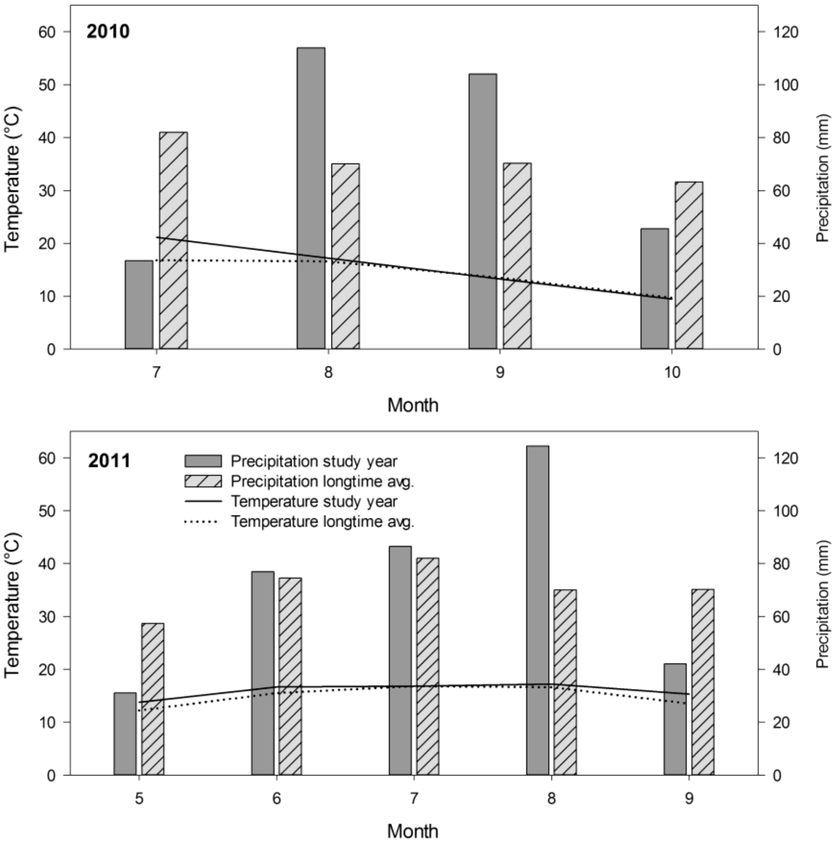

Fig. 5.1: Sums of monthly precipitation and mean daily temperatures per month for the period of the experiments and the long time averages of these variables (data of the nearest weather station Hamburg Fuhlsbüttel from the DWD 2012)

For the sod experiment, the sods of floodplain meadows were also planted into 1-m high pots, which were filled with standard garden soil. These pots were also randomly distributed onto the three different levels in the two above-mentioned water basins to simulate groundwater levels of 20, 40 and 60 cm below soil surface (see Fig. 5.2). The water levels were kept constant throughout the experiment, in the same way as for the experiment without competition. In the sod experiment, pots with a diameter of 15 cm were used to ensure enough root material of the plants in the sods of floodplain meadows. This led to 10 replicates per water level and origin. The sod experiment was conducted from May to September 2011. To simulate mowing, plants in the sods were clipped two times during the experiment in July and September 2011.

To analyse if the experimental water levels led to significant differences in soil moisture at the surface of the pots, we measured the soil moisture using the TDR technique. Soil moisture was measured in all pots on the 3rd and 9th of September 2011 after three dry and three rainy days, respectively.

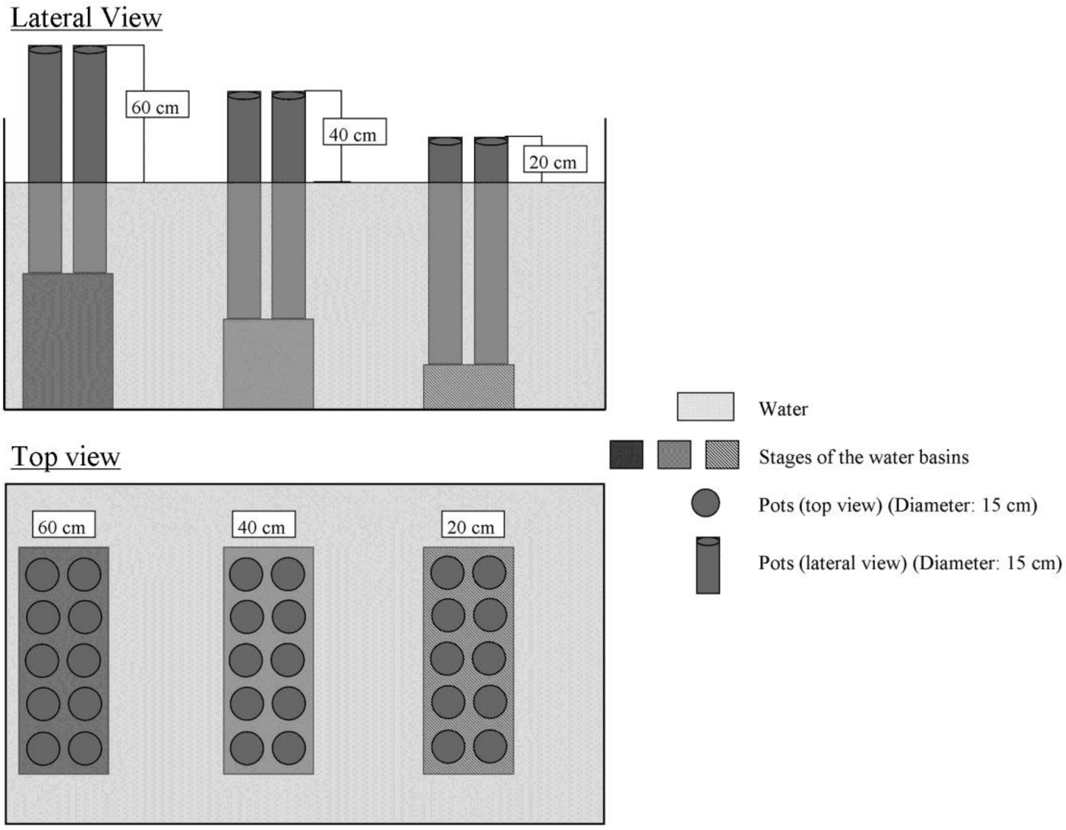

Fig. 5.2: Setup of the sod experiment with competition in water basins (length: 3 m; width: 1.5 m; height: 1.5 m) with ten pots on each stage. In the experiment without competition, 20 pots were arranged on each stage

Performance of **C. dubium** *and competitors*

We selected length of longest leaf and biomass as traits to evaluate the plants performance. Leaf size has been previously shown to respond to prevailing hydrological conditions (Givnish and Vermeij 1976). Biomass can be regarded as a proxy for plant fitness, which is difficult to measure directly in clonal plants.

In the experiment without competition, the length of the longest leaf of *C. dubium* was measured monthly from August to October 2010. The plants in the pots were clipped at the end of the experiment in October 2010. In Winter 2010/2011, the belowground biomass i.e. the roots were sieved and washed out of the soil. Above- and belowground biomass was dried at 60 °C for three days to measure dry weight per pot.

In the sod experiment, the length of the longest leaf of *C. dubium* was measured monthly from June to September 2011. Additionally, the cover of *C. dubium* and its competitors was estimated on a monthly basis using the Londo-scale (Londo 1976). The plants in the pots were clipped at the mowing dates in July and September, and the resulting aboveground biomass was sorted into the groups *C. dubium* and competitors. The aboveground biomass of this experiment was also dried at 60 °C for three days to measure dry weight per pot.

Besides water level and competition, we wanted to analyse the influence of origin on the performance of *C. dubium*. This was possible in the experiment without competition, because all individuals were grown at standardised conditions from seeds originating from two sites differing in climatic conditions. In the sod experiment, we could not look for differences in sod origin as origin was possibly confounded with soil conditions and ramet age.

Statistics

In the experiment without competition, the effects of water level ($k = 3$), origin ($k = 2$) and basin ($k = 2$) on the biomass of *C. dubium* was tested using a three-factorial ANOVA. The third factor, basin, was included to account for possible effects of the two used basins on the measured response variable. To account for temporal changes in the length of longest leaf of *C. dubium,* we conducted a repeated measurement ANOVA. In the sod experiment, the effects of water level ($k = 3$) and basin ($k = 2$) on the variables length of longest leaf, biomass of *C. dubium,* and biomass of its competitors were tested using repeated measurement ANOVAs. Additionally, we included the number of competitive species in each pot as a co-variable to the repeated measurement ANOVAs, analysing the response variables length of longest leaf and biomass of *C. dubium*. The effect of the experimental water levels on soil moisture was also analysed with repeated measurement ANOVAs. If results were significant, a Fisher LSD post hoc test was conducted for pair-wise comparisons. Data transformations (log + 1, log + lowest value of the data set, square-root) were conducted to approximate normal distribution and variance homogeneity. Where this was not possible, non-parametric tests were used: In the pots (sod experiment), the cover of *C. dubium* and some of the most frequent competitors (namely *Alopecurus pratensis, Phalaris arundinacea, Poa pratensis, Potentilla reptans* and *Vicia cracca*) were analysed with Kruskal –Wallis ANOVAs. These competitors were chosen because they had at least 14 occurrences, equally distributed on the three tested water levels at the beginning of the experiment. If cover was significantly affected by water level, pair-wise Mann –Whitney U Tests were conducted as post hoc tests (Dytham 2003). All statistical analyses were conducted using STATISTICA 9.1 (StatSoft, Inc.).

Results

Experimental water levels and soil moisture

The artificial water levels of the experiments (20, 40 and 60 cm) were approximately in the same range as the groundwater levels during summer in the meadows from which seeds and sods originated (Table 5.1). The experimental water levels led to significant differences in soil moisture at the surface of the pots ($F_{2,54} = 144.1$; $p < 0.001$; Table 5.2). Additionally, soil moisture was significantly lower on 3rd of September 2011 after three dry days than on 9th of September 2011 after three rainy days (time: $F_{1,54} = 33.3$; $p < 0.001$).

Table 5.2: Soil moisture measured with TDR technique in the pots at the three experimental water-levels (20 cm, 40 cm, 60 cm).

Date	Water level (cm)	Soil moisture mean ± SD (Vol%)	Water level 20 cm	Water level 40 cm
09/03/2011	20	54.1 ± 3.9		
09/03/2011	40	41.6 ± 4.1	***	
09/03/2011	60	32.0 ± 6.9	***	***
09/09/2011	20	57.8 ± 4.3		
09/09/2011	40	43.3 ± 4.9	***	
09/09/2011	60	35.1 ± 5.8	***	***

Pairwise differences regarding Fisher LSD test results for each date of measurement (3rd and 9th of September 2011 after three dry days and three rainy days, respectively). *** = p<0,001

Effects of water level and origin on juveniles of C. dubium

Water level had a significant effect on the length of the longest leaf of *C. dubium* in the experiment without competition ($F_{2,108} = 5.8$; $p < 0.01$). The leaves were significantly shorter at water level 60 cm compared to 40 cm (see Fig. 5.3a). Overall, the longest leaves of *C. dubium* were developed at water level 40 cm, but the difference to water level 20 cm was not significant. These relations did not change over time (time x water level: $F_{4,216} = 0.5$; $p = 0.76$).

The aboveground biomass of *C. dubium* juveniles was significantly affected by water level ($F_{2,108} = 3.3$; $p < 0.05$; Fig. 5.3b). At water level 20 cm, the aboveground biomass was significantly lower than at water level 40 cm and 60 cm (both $p < 0.05$). The belowground biomass of *C. dubium* juveniles was also significantly affected by the water level ($F_{2,86} = 5.3$; $p < 0.01$; Fig. 5.3c). At water level 20 cm, the belowground biomass was significantly lower than at water level 40 cm ($p < 0.01$). The ratio (aboveground/belowground biomass) was not affected by water level ($F_{2,86} = 1.1$; $p = 0.35$).

Furthermore, seed origin significantly affected leaf length ($F_{1,108} = 24.3$; $p < 0.001$; Fig. 5.4a), aboveground biomass production in October 2010 ($F_{1,108} = 4.3$; $p < 0.05$; Fig. 5.4b) and belowground biomass ($F_{1,86} = 4.2$; $p < 0.05$; Fig. 5.4c). *C. dubium* juveniles originating from the more continental Havel River always had longer leaves ($p < 0.05$ for all month) and produced more biomass ($p < 0.05$) than the individuals from the more oceanic Sude River.

However, we did not detect a significant origin –environment interaction: The response of aboveground biomass ($F_{2,108} = 0.8$; $p = 0.46$) and leaf length ($F_{2,108} = 0.3$; $p = 0.74$) of the plants with different origin did not change along the tested water level gradient.

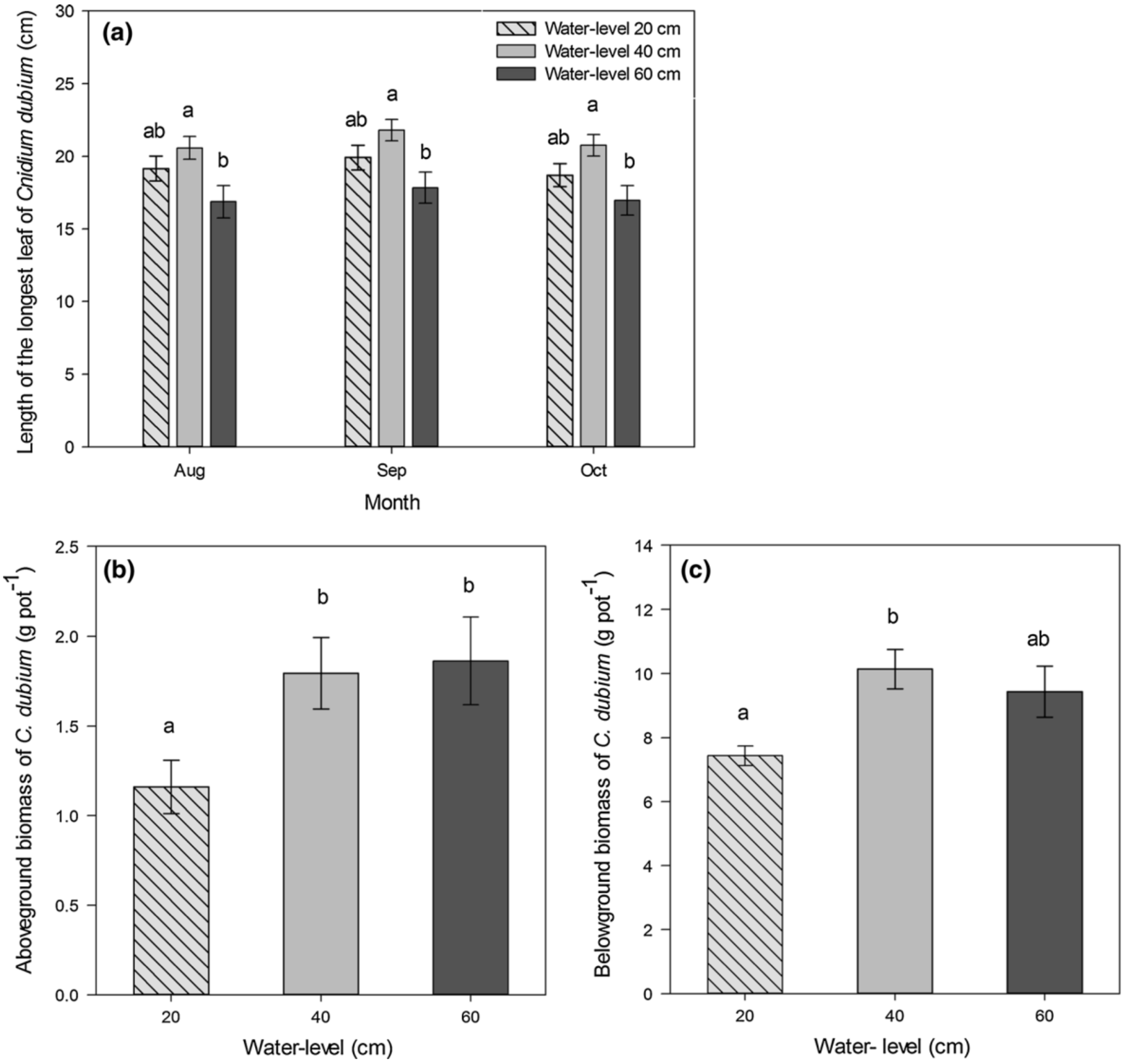

Fig. 5.3: Experiment without competition: **a** Length of longest leaf of *Cnidium dubium* according to water level (20, 40 and 60 cm) (mean ± SE) shown for each month of measurement. Letters refer to significant differences within month. **b** Aboveground and **c** belowground biomass of *Cnidium dubium* according to water level (20, 40 and 60 cm) at the end of the experiment (October 2010) (mean ± SE)

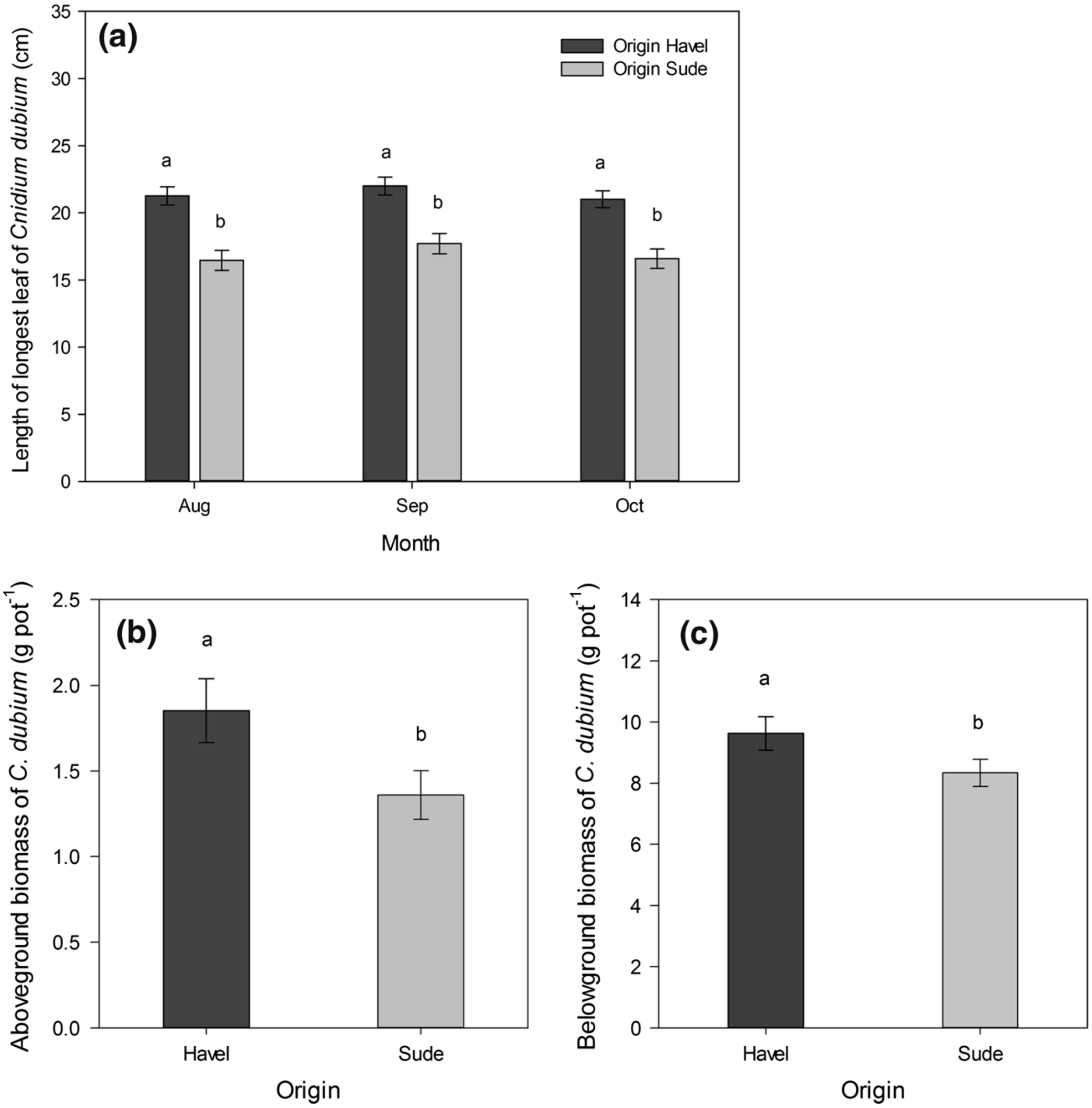

Fig. 5.4: Experiment without competition: **a** Length of longest leaf of *Cnidium dubium* according to origin of the seeds (Havel, Sude) (mean ± SE) shown for every month of measurement. Letters refer to significant differences within month. **b** Aboveground and **c** belowground biomass of *Cnidium dubium* according to origin of the seeds (Havel, Sude) at the end of the experiment (October 2010) (mean ± SE)

Effects of water level on **C. dubium** *in sods*

In the sod experiment, the length of the longest leaf of *C. dubium* was significantly affected by water level ($F_{2,53} = 4.4$; $p < 0.05$), yet the effect of water level changed over time ($F_{6,159} = 13.5$; $p < 0.001$; Fig. 5.5a). In June and July, *C. dubium* had the longest leaves at water level 20 cm. After clipping, these patterns changed in August and September: the leaves were longest at water level 40 cm and 60 cm, but this effect was only significant between water level 20 cm and 60 cm in August.

The same shift appeared for the cover of *C. dubium,* which changed over time (data not shown): In July, water level had a significant effect ($H = 7.8$; $p < 0.05$): Here, cover was significantly higher at water level 20 cm compared to 40 cm and 60 cm (both $p < 0.05$). After clipping, *C. dubium* had a significantly lower cover at water level 20 cm compared to 40 cm and 60 cm, both in August ($H = 14.3$; $p < 0.001$; 20 vs 40 cm: $p < 0.001$ and 20 vs 60 cm: $p < 0.01$) and in September ($H = 10.8$; $p < 0.01$; 20 vs 40 cm: $p < 0.01$ and 20 vs 60 cm: $p < 0.05$).

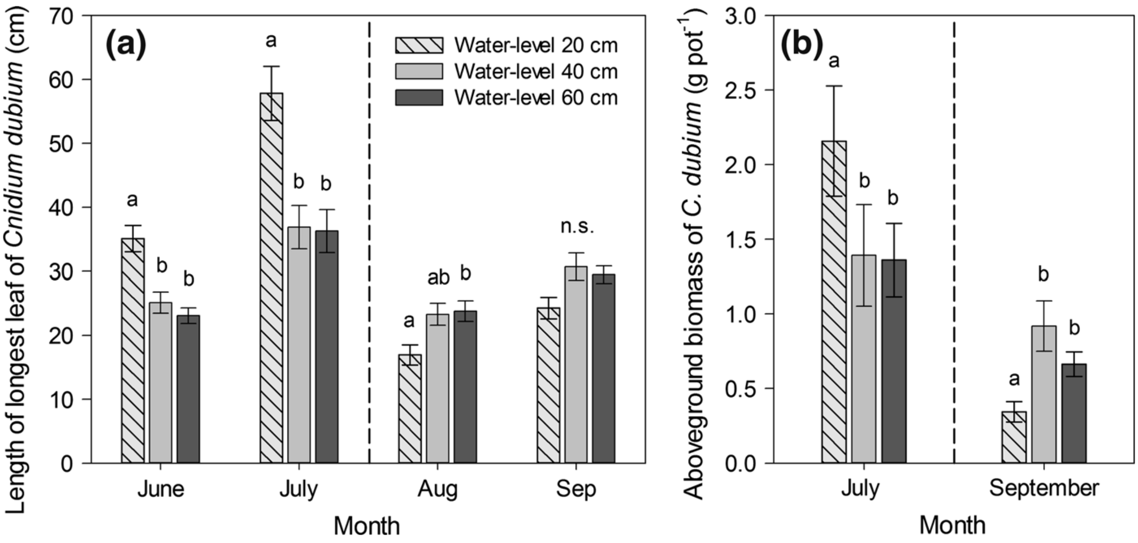

Fig. 5.5: Sod experiment: **a** Length of longest leaf of *Cnidium dubium* according to water level (20, 40 and 60 cm) (mean ± SE) shown for every month of measurement. Letters refer to significant differences within month. (n.s. not significant). Biomass was clipped between measurements of July and August and after the measurements of September 2011. **b** Biomass of *Cnidium dubium* according to water level (20, 40 and 60 cm) in July and September 2011 (mean ± SE). Dashed line refers to clipping date

Additionally, this shift appeared in the aboveground biomass of *C. dubium*. The effect of water level changed over time ($F_{2,53} = 12.3$; $p < 0.001$; Fig. 5.5b). The aboveground biomass of *C. dubium* was significantly higher at water level 20 cm compared to water level 40 cm and 60 cm (both $p < 0.05$) in July, while it was significantly less at water level 20 cm compared to water levels 40 cm ($p < 0.001$) and 60 cm ($p < 0.01$) in September.

Likewise, the aboveground biomass of the competitors of *C. dubium* was affected by the interaction of water level and time ($F_{2,48} = 5.1$; $p < 0.01$; Fig. 5.6). In July, biomass of competitors tended to be highest at water level 20 cm. In September, most biomass grew at water level 60 cm, but the difference was only significant between water level 20 cm and 60 cm. Thus, *C. dubium* always had its longest leaves, highest cover and highest biomass where its competitors had the highest biomass. The co-variable number of competitive species per pot had no significant effects on length of longest leaf and aboveground biomass of *C. dubium*.

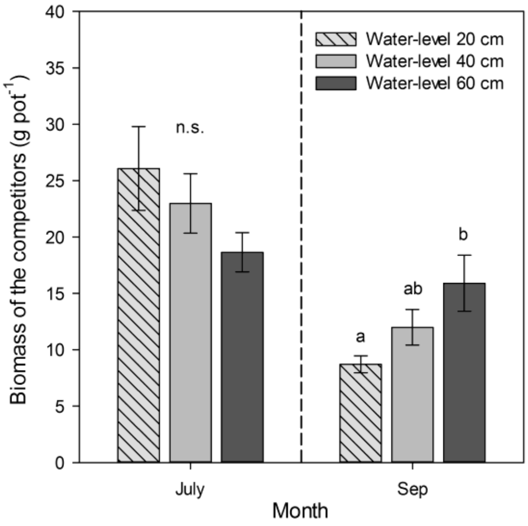

Fig. 5.6: Biomass of the competitors of *Cnidium dubium* in the sod experiment in July and September 2011 (according to water levels 20, 40 and 60 cm; mean ± SE). Letters refer to significant differences within month (n.s. not significant). Dashed line refers to clipping date

The most frequent species *Alopecurus pratensis, Phalaris arundinacea, Poa pratensis, Potentilla reptans* and *Vicia cracca* were not affected in their cover by the water level in any of the month investigated (all $p > 0.05$; data not shown).

Discussion

Effects of water level on C. dubium

The performance of *C. dubium* is affected by the water level, either with or without competition. In the experiment without competition, the species displayed its best performance at a water level of 40 and 60 cm below soil surface: biomass was highest at these water levels and the longest leaves were developed at water level 40 cm. Therefore, water levels in this range during summers can be considered as the physiological optimum for this species.

Under competition, the leaves of *C. dubium* were always longest, and its biomass and cover were the highest at that water level with the highest biomass production of the competitors. *C. dubium* developed longer leaves and had a higher cover and biomass at water level 20 cm in June and July, while in August and September it tended to develop longer leaves and had higher cover and biomass at water level 60 cm. A possible reason could be that clipping of aboveground biomass in the pots has changed the competitive relations between the meadow plants. Lenssen et al. (2004) report that disturbance can lead to competitive change. The competitive change hypothesis indicates that species could change their position in the competitive hierarchy after disturbances (Suding and Goldberg 2001). However, as *C. dubium* always showed the longest leaves, highest cover and highest biomass where competitor biomass was also highest, its position in the competitive hierarchy was unaltered after clipping. Indeed, the whole plant community changed its best performance to another water level over the months, which might be explained by the precipitation pattern of 2011: While precipitation in May and June was overall lower than the long-term average (Fig. 5.1), the plants grew best at the wettest water level (20 cm). In August and September, when precipitation was higher overall than the long-term average (Fig. 5.1), plants grew best at the driest water level (60 cm).

Whatever reason was responsible for this shift, our finding that *C. dubium* always developed the longest leaves at the water level with the highest biomass of competitors is probably most important. This matches with the results of Gaudet and Keddy (1988) and Keddy (1990), who concluded that plants develop the longest leaves where competition is highest as an adaptation to the prevailing light conditions.

Overall, we demonstrated that *C. dubium* has an optimal range of water levels during summer (in the experiment without competition), but was able to respond plastic to different competitors' biomasses (in the sod experiment). This is positive evidence for the endangered *C. dubium* in times of climate change, as species which show pronounced phenotypic plasticity might adapt better to the effects of climate change (Nicotra et al. 2010; Pauls et al. 2012).

Effects of seed origin

We found clear differences in growth between the *C. dubium* plants with different origins (with plants from the more continental Havel site outperforming those from the Sude site). These differences were detectable among all applied water levels. The results indicate that the individuals of *C. dubium* growing on the grasslands along the Havel and Sude Rivers might not belong to the same population. This indicates that dispersal along the Elbe River is limited, although hydrochory is usually considered to operate as a strong dispersal process (Vogt et al. 2006; Michalczyk et al. 2011). Furthermore, the performance differences in the plants of the two origins display pronounced trait variability in *C. dubium*. Whether this variability is due to local adaptations or epigenetic effects is impossible to disentangle within the scope of our study. The intraspecific trait variability of *C. dubium* might be evidence of its ability to adapt to changing conditions (Jump et al. 2009; Pauls et al. 2012). Research is needed on the intraspecific genetic variation of *C. dubium* (Michalczyk et al. 2011) and its implication for survival under changing environmental conditions.

Implications for nature conservation

The river corridor plant *C. dubium* performed best at groundwater levels of 40 – 60 cm below soil surface, which is close to the mean groundwater level of its natural habitat during hydrological summer. Our findings demonstrate that water level differences of some 10 centimetres already had significant effects on the growth of this species. Therefore, we assume that future water level reductions due to less summer precipitation could exhibit an effect on the positioning of *C. dubium* in floodplain grasslands. However, the intraspecific trait variability of *C. dubium* indicates an ability to cope with at least moderate effects of climatic change in its present habitats. We have to admit, however, that neither the upper nor the lower limit of the groundwater level range, at which *C. dubium* occurs in functional floodplains, was represented in our experiments. Recently, it has been shown that extreme events might play a major role in ecosystem functioning (Jentsch et al. 2011). We are not able to extrapolate our results to extreme conditions or to water levels deviating strongly from today's mean groundwater range.

If a management procedure becomes necessary for the conservation of the endangered river corridor plant *C. dubium* as a result of future climate change, setting up a groundwater level of 20 cm to 60 cm below soil surface in floodplain meadows during summers might be a suitable adaptation strategy to prevent drought stress and facilitate the conservation of *C. dubium*. Already today, hydrological management, including raising the groundwater table, is a method to conserve endangered plant species in the wet grasslands of Europe (Toogood and Joyce 2009). For Elbe River tributaries, this would be possible where there are weirs for managing grassland drainage. As an alternative approach, drainage in floodplain grasslands could be reduced by filling ditches. As we also found that the tested water levels had no negative effect on the cover of the most frequent competitor species, we conclude that setting up a water level within this range would not have negative impacts on these species. Overall, the maintenance or restoration of the dynamic hydrological conditions of floodplains appears to be crucial for the conservation of river corridor species (Toth and van der Valk 2012) and an essential prerequisite for any management strategy to mitigate the negative impacts of climate change in floodplain ecosystems.

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CHAPTER 6

POSSIBLE EFFECTS OF CLIMATE CHANGE OF THE VEGETATION OF FLOODPLAIN MEADOWS – SYNTHESIS

Kristin Ludewig

Key findings of this thesis

This section summarizes the key findings for the research objectives this thesis is based on (see chapter 1). The four objectives were (1) analyzing the current influence of climate on the vegetation of floodplain meadows, (2) analyzing the effects of reduced water potentials on the germination of floodplain meadow species, (3) analyzing the effects of reduced summer precipitation on the forage quality of floodplain meadows, and (4) analyzing the effects of water level and competition on an endangered river corridor plant.

1.1) The vegetation composition of wet meadows (but not of mesic meadows) changed along the climatic gradient at the Middle Elbe River. While the species number did not differ between sites in either of the meadow types, evenness of species was higher in the western sites compared to the eastern ones in the mesic meadows.

1.2) Changes in vegetation composition of the wet meadows along the Middle Elbe River were correlated with climatic variables, especially with temperature and precipitation variables.

1.3) Plant species with a rather continental distribution did not occur in higher abundance in the eastern part of the studied gradient along the Elbe River. It was *vice versa*, in mesic meadows more plant species with a rather continental distribution grew in the western part of the gradient.

1.4) Accordingly, river corridor plants were more abundant in the western sites compared to the eastern sites of the gradient (although this finding was only significant for the mesic meadows).

2.1) The experimentally reduced water potentials reduced the germination of all studied plant species of floodplain grasslands.

2.2) The temperature regime affected the germination patterns of the species. The seeds of most species germinated faster at the lower temperature regime 15/5 °C compared to 20/10 °C.

2.3) Seeds originating from populations at the Elbe River did not differ in their response to reduced water potentials, compared to those from populations along the Rhine River.

2.4) Germination of the species indicative of dry habitats decreased more strongly, and was slower and less synchronous at reduced water potentials than that of species indicative of wet habitats.

3.1) Reduced summer precipitation of 50 % affected the productivity of the floodplain meadows negatively in the second cut at the Rhine River. Precipitation reductions of 25 % had no effect on the productivity at either of the study regions.

3.2) The quality of hay was affected in the second annual cut at 50 % precipitation reduction at the Rhine River. While the energy content and crude protein rose, the crude fibre content decreased in the hay at 50 % less precipitation.

3.3) The overall annual energy yield of floodplain meadows (of the first and second cut together) decreased at 50 % precipitation reduction at the Rhine River.

4.1.) Without competing plants, *Cnidium dubium* performed best at the water levels of 40 – 60 cm below soil surface during summer.

4.2.) Under competition, the performance of *C. dubium* was always best at the water level with the highest biomass production of the competitors. During the experiment, the favorable water level for *C. dubium* and its competitors changed.

4.3.) The juveniles grown from seeds of different origins did not differ in their response to the applied water levels, but they differed in their growth from each other, indicating local adaptations or genetic differentiation between the two populations.

Possible effects of climate change on the vegetation of floodplain meadows

How may climate change affect the vegetation of floodplain meadows? This remains a tough question, due to the multiple environmental factors which combine to affect the floodplain ecosystems. The results of this thesis indicate that the effects of today's climatic gradient on the vegetation at the Elbe River were rather small (chapter 2). Furthermore, the influence of reduced summer precipitation on the forage quality of meadow vegetation was rather limited (chapter 4). However, the effects of three water levels (differing only by a few decimeters) on the performance of the river corridor plant *Cnidium dubium* was pronounced (chapter 5). Therefore, it can be stated that the indirect influence of climate change, i.e. the changing river discharges due to changing precipitation regimes with the resulting changing water levels in the floodplains, appears to be the most influential factor for floodplain vegetation. This fits with Catford *et al.* (2013), who stated that changes in stream discharge are likely to have the largest influence on floodplain ecosystems. Here, it has to be kept in mind that the Elbe and Rhine Rivers generally have different stream flow characteristics. While the discharge regime of the Middle Elbe River is a snow-rain system (depending on snow melt and rain events), the discharge regime of the Upper Rhine is a snow system (Nilson *et al.* 2014). Therefore, the Elbe and Rhine Rivers may differ in their future discharge changes due to climate change (Nilson *et al.* 2014).

If the mean summer discharges of the Elbe and Rhine Rivers were to decrease permanently (and consequently the groundwater table in the floodplains), the plant species might follow this environmental shift, down the elevation gradient in the functional floodplains. This can be assumed, as some plant species of floodplain meadows slightly shift along the elevation gradient in response to annual hydrologic conditions (Vervuren et al. 2003, Redecker 2004). However, it is unclear if the plant species of floodplain meadows are able to follow future water level reductions. The same is true for the question of whether or not the extent of the vegetation zones will remain the same as today. Several studies (Rood *et al.* 2008; Ström *et al.* 2011; Rivaes *et al.* 2013) indicate that the vegetation zones may get squeezed when the water level amplitude decreases and get larger when the water level amplitude increases.

Two of the studies within this thesis were conducted on wet and mesic meadows or with seeds of species from wet and dry floodplain grasslands (chapter 2 and 3). Which type of meadow appears to be more vulnerable to climatic change? In the study on the vegetation composition along the regional climatic gradient at the Elbe River, the wet meadows exhibited clearer patterns than the mesic meadows, in relation to the climatic variables (chapter 2). Accordingly, in the study of the germination responses to reduced water potentials, the species indicative of wet meadow habitats seemed to be more negatively affected by reduced water potentials than those of dry meadow habitats. The seeds of species from wet habitats were not able to sense the reduced water potential in their surroundings, and germinated readily in conditions that were unfavourable for establishment. However, the species indicative of dry meadow habitats were able to detect the moisture regime in their surroundings, and germinated later, more asynchronous and less often in dry (and thus unfavorable) conditions for establishment. Further, more extreme rainfall events could lead to a higher frequency of flooding events during the vegetation period. These altered conditions would especially challenge the plant species typical of wet areas in the floodplains, and may often lead to damage or loss of individual plants in the aftermath. All in all, it can be assumed that the species of wet meadow habitats are more vulnerable to the impacts of potential droughts and more frequent future flooding events.

Implications for conservation of floodplain meadows under climate change

What can be done for the conservation of floodplain meadows under climate change? Overall, the dynamic conditions of a functional floodplain appear to be an essential prerequisite for any intact floodplain ecosystem (e.g. Naiman *et al.* 1993). This will also hold true under changing climatic conditions. Therefore, the maintenance or restoration of functional floodplain areas remains an urgent need. Accordingly, Erwin (2009) highlights the importance of protecting and restoring species-rich wetland ecosystems, in order to improve their resilience to changing climatic conditions. Another feature that helps to mitigate negative impacts of climatic change is small scale heterogeneity in landscapes. Different micro-habitats lying at small distances may offer species temporarily suitable habitats (Harris *et al.* 2006). Small distances are likely to be reached by most floodplain species via dispersal (Burmeier *et al.* 2011). As small scale heterogeneity is a characteristic of floodplain ecosystems, this is another argument for their conservation and restoration.

One way in which larger areas of floodplain meadows facilitate a better adaptation capacity of rare floodplain species is by providing more suitable habitats. Larger habitats can potentially be inhabited by larger populations of these species. Larger populations, in turn, could increase the genetic variability of a species, which is known to be of advantage in adapting to new conditions (e.g. Aguilar *et al.* 2008). Furthermore, larger populations could potentially produce more seeds, which could possibly be dispersed to new suitable habitats. All in all, larger populations help species to ‘adapt or disperse’, the two possible ways of reducing the probability of extinction (Berg *et al.* 2010).

If negative effects of climate change, i.e. prolonged water deficit conditions, become perceivable in the floodplain ecosystems, necessitating a management procedure for the conservation of endangered river corridor plants, such as *C. dubium*, then the results of the water level experiment (chapter 5) are important. Setting up a groundwater level of 20 cm to 60 cm below soil surface in floodplain meadows during summers might be a suitable adaptation strategy to prevent drought stress and facilitate the conservation of *C. dubium* and other river corridor plants. Already today, hydrological management, including raising the groundwater table, is a method for conserving endangered plant species in wet grasslands of Europe (Toogood & Joyce 2009). For Elbe River tributaries, this would be possible where weirs are used for managing grassland drainage. As an alternative approach, drainage in floodplain grasslands could be reduced by filling ditches. As the study (chapter 5) also found that the tested water levels had no negative effect on the cover of the most frequent competitor species, setting up a water level within this range would probably not negatively affect these species. As already mentioned above, the maintenance or restoration of the dynamic hydrological conditions of floodplains appears to be the first priority for the conservation of river corridor species (Toth & van der Valk 2012) and essential for any strategy to mitigate the negative impacts of climate change in floodplain ecosystems.

Perspectives for future research

How should future research proceed? According to the studies of this thesis, recommendations and ideas for future work can be put forward. Considering the germination study of floodplain grassland species (chapter 3), it would be necessary to test if the interpretation of our results holds true under field conditions. We proposed that species of wet sites follow an all-or-nothing-strategy, with fast and synchronous germination to maximize competitive advantages, betting on a high probability of moist conditions for establishment (optimists). In contrast, species from dry sites appear to follow a bet-hedging strategy, with a moisture-sensing mechanism for unsuitable conditions (pessimists), resulting in slower and less synchronous germination. Analysis of this topic should include controlled manipulation of the soil water potentials in the field, which is a challenging task for future research.

Manipulating the soil moisture in the field was also relevant in the precipitation reduction experiments with rainout shelters (chapter 4). The problem in these experiments was either that it sometimes did not rain at all (larger periods in 2009 at the Elbe River tributaries), or the water level of the river was continuously high (leading to three small flooding events in 2010 at the Elbe River tributaries). Consequently, during these times there were no differences in the soil moisture of the plots with and without precipitation reduction. Therefore, the effects of reduced precipitation may be underestimated with this experimental approach. Generally, it would be recommendable to run such experiments for longer periods of time, in order to level out annual weather conditions. Besides this, it would be meaningful to include the effects of higher rainfall variability that, for instance, had a large influence on the productivity of North American grassland (Knapp *et al.* 2002). For Central Europe too, climate change models project higher rainfall variability with longer durations without rain, as well as more extreme rainfall events (Jacob *et al.* 2008; Rechid 2014).

Apart from the studies presented in this thesis, other topics appeared to be important for future research. One such topic is the fluctuation of vegetation zones in floodplain grasslands. Specific zones of plant communities can be found along the elevation gradient in floodplains (Leyer 2002). These vegetation zones are the result of abiotic factors (e.g. soil moisture, groundwater level and amplitude, and flooding frequency) and biotic factors (e.g. competition). As a next step it would be required to investigate whether (and to which extent) vegetation zones shift along the elevation gradient over years due to annual weather differences. Additionally, an assessment could be made of how future weather variability and water level changes influence the vegetation zones.

Another possible topic for future research could be the time between the mowing of the floodplain meadows and the flooding events. A personal observation in the floodplains of the Elbe and Rhine Rivers was that most plant species cope better with summer flooding events when they are larger in height. This topic would require further research, as a possible management strategy might be to not cut meadows when a flooding event is foreseeable.

Floodplains are fascinating ecosystems of high nature conservation value. With their unique mixture of wet and dry conditions on small scales, floodplains offer diverse habitats for flora and fauna, and ample opportunities for scientists to analyze plant responses to conditions ranging from water deficits to anoxia.

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Summary

Floodplains are dynamic and productive ecosystems with diverse plant and animal communities, and are considered hot spots of biodiversity. The dynamic conditions of floodplains can be characterized by the interplay of wet conditions during regularly or irregularly occurring floods, mainly in winter and spring, and dry conditions over the summer. These hydrologic conditions give rise to distinct zones of plant communities along the elevation gradient in floodplains. Due to the tightly intermingled vegetation zones, species density is generally high. Furthermore, European floodplains harbor many rare and endangered plant species, such as river corridor plants, especially in the floodplain meadows. However, species-rich floodplain meadows have declined strongly over recent centuries due to habitat loss, mainly caused by land-use changes, river regulations, and river training. Consequently, the remaining species-rich floodplain meadows are of high conservation value, protected under the European Habitats Directive, and subject to various restoration measures.

Climate change might pose an additional threat to the persistence of species-rich floodplain meadows. For western and northern Germany, regional climate change projections indicate higher temperatures and an increasing risk of summer droughts for the late 21st century, due to less summer precipitation in relation to the reference period 1961-1990. Accordingly, reduced river discharges during summers are projected for the rivers Rhine and Elbe. This, in turn, would lower the groundwater table in the adjacent floodplains, with negative effects on the soil water potential. It is still largely unknown whether and how the vegetation of floodplain meadows will be affected by direct climatic changes (such as higher temperatures and reduced summer precipitation) and indirect effects due to climate change (such as water level changes in the floodplains).

The overall aim of this thesis was to elucidate the possible effects of climate change on Central European floodplain meadows. Therefore, four research objectives were addressed: (1) identifying the current influence of climate on the vegetation of floodplain meadows, (2) elucidating the effects of reduced water potentials on the germination of floodplain meadow species, (3) quantifying the effects of reduced summer precipitation on the forage quality of floodplain meadows, and (4) disentangling the effects of water level and competition on the endangered floodplain meadow species *Cnidium dubium*.

In the first study, the vegetation of floodplain meadows along the regional climatic gradient of the Middle Elbe River (Germany) was examined (chapter 2). This gradient exhibits oceanic conditions in the north-west, whilst rather continental conditions prevail in the south-east. The aim of this study was to detect the influence of climate on the vegetation of wet and mesic meadows along this gradient. If a climatic influence was detected, then climate change may also have an effect in the future on the vegetation of floodplain meadows. The vegetation of wet and mesic meadows was recorded on overall 46 plots from Bleckede to Wörlitz in 2010. The results revealed differences in species composition, especially in wet meadows: Vegetation plots of wet meadows clustered in the DCA-ordination according to their geographic location from west to east. Sample scores of

DCA-axes of both meadow types correlated with the long-term means of climatic factors, such as precipitation and temperature. Indicative species of the sites were mainly common meadow species, whereas species typical for floodplain meadows were relatively evenly distributed along the gradient. Therefore, it can be confirmed that the regional distribution of typical floodplain species is largely determined by hydrologic and land-use conditions, rather than by climatic factors. Typical floodplain meadow species at the Elbe River appear to be relatively robust in the face of direct climatic changes, as long as these changes do not exceed the range of today's climatic gradient. Concerning the total plant assemblages of floodplain meadows, those of wet meadows might be more vulnerable to climate change than those of mesic meadows. However, indirectly occurring changes caused by climate change will affect all floodplain species, i.e. water-level changes due to an altered discharge regime of the Elbe River, caused by altered precipitation patterns in the catchment.

While adult plants can often withstand even strong environmental changes, early life phases might be more vulnerable, such as seed germination and seedling establishment. Therefore, an experiment was carried out in the second study to see whether reduced soil water potentials would affect the germination of meadow species, and whether the response varies between forbs indicative of wet and dry habitats or between seeds originating from the rivers Elbe and Rhine (chapter 3). We exposed seeds of 20 floodplain meadow species with different moisture requirements from five plant families to a water potential gradient ranging from 0 to -1.5 MPa at two temperature regimes (5/15 °C and 10/20 °C). Seeds from five species were collected at both the Elbe and Rhine Rivers. Overall, germination percentage and synchrony decreased, and germination time increased at reduced water potentials. Germination of the species indicative of dry habitats decreased more strongly, was slower, and less synchronous at reduced water potentials than that of species indicative of wet habitats. Seeds from the rivers Elbe and Rhine did not differ in their germination characteristics. We propose that species of wet sites follow an all-or-nothing-strategy, with fast and synchronous germination to maximize competitive advantages, betting on a high probability of moist conditions for establishment (optimists). In contrast, species from dry sites appear to follow a bet-hedging strategy, with a moisture-sensing mechanism for unsuitable conditions (pessimists), resulting in slower and less synchronous germination. Their 'pessimistic' response (germinating only when they sense sufficiently moist conditions) probably enables them to track the time windows with a high probability for successful germination and establishment. Seeds of species indicative of wet habitats do not possess such a mechanism, since the conditions in their typical habitat are usually sufficiently moist. Their 'optimistic' response to this environmental factor probably makes them comparably vulnerable to climate change.

As floodplain meadows depend on regular land-use, climate change effects on the quantity and quality of the harvested forage were investigated in the third study (chapter 4). Field experiments were conducted to analyze the effects of reduced summer precipitation on the amount and quality of the harvested forage of floodplain meadows at two Elbe tributaries (25 % rain reduction from 2009-2011) and at the Rhine River (25 % and 50 % rain reduction from 2011-2013). The following variables were measured: the amount of hay biomass, its contents of crude protein, crude fibre, energy, fructan, nitrogen, phosphorus,

and potassium, and the annual yield (biomass * energy content). Overall, the annual yield decreased at the Rhine River at 50 % rain reduction, but not at 25 % reduction at both rivers. In the first cut, the quantity and quality of the floodplain meadow hay were almost not affected by the experimental treatments at either of the rivers. The second cut from the Elbe River was also only marginally affected by the experimental treatments. In contrast, the amount of floodplain meadow hay from the second cut at the Rhine River decreased at precipitation reduction of 50 %, while its contents of nitrogen and crude protein increased. That the first cut was almost unaffected by the precipitation reduction is probably due to sufficient soil moisture from winter/spring. As the first cut is more important for agricultural purposes, these results indicate that the use of floodplain meadows might be sustainable under (moderate) future climate change. Nevertheless, these results only hold as long as the water levels of the rivers do not decrease in future during spring, and as long as the precipitation reduction during summer is not too severe (< 25 %).

Besides direct climatic changes, indirect climate change effects, such as water level changes, can also occur in floodplains due to precipitation alterations. In the fourth study, the aim was thus to test how the characteristic floodplain meadow plant *Cnidium dubium* responds to water level changes, and to develop implications for its management in the course of climate change (chapter 5). Two mesocosm experiments were set up with plants originating from floodplain meadows along two tributaries of the Elbe River, Germany. In the first experiment, growth characteristics and biomass of juvenile *C. dubium* individuals were investigated in response to groundwater level (20, 40, and 60 cm below soil surface) and origin (floodplains at the Sude and Havel River). In the second experiment, competitors were included to analyse interactive effects of competition and water level on mature plants of *C. dubium*. Growth of *C. dubium* was affected by the water level, with a physiological optimum at water levels of 40 – 60 cm below soil surface. *C. dubium* showed genetic differences between the populations of the sites of seed origin and evidence of phenotypic plasticity in relation to competition. We suggest raising the groundwater level to 20 – 60 cm below soil surface as a possible management strategy, when drought (as a consequence of climate change) is perceivable.

Overall, the results presented in this thesis indicate that the indirect influence of climate change, i.e. the changing river discharges due to changing precipitation regimes - with the resulting changing water levels in the floodplains, appears to be the most influential factor for floodplain vegetation. As two studies of this thesis were conducted on wet and mesic meadows, or with seeds of species from wet and dry floodplain grasslands, the responses of the two species groups can be compared. All in all, it can be assumed that the species of wet meadow habitats will be more vulnerable than the species of dry meadow habitats to the impacts of potential droughts in the future.

If negative effects of climate change become perceivable in the floodplain ecosystems, e.g. prolonged water deficit conditions, a management procedure might become necessary for the conservation of the endangered river corridor plants, such as *C. dubium*. Setting up a groundwater level of 20 cm to 60 cm below soil surface in floodplain meadows during summer might be a suitable adaptation strategy to prevent drought stress and facilitate the conservation of *C. dubium* and other river corridor plants. Overall, the dynamic conditions

of a functional floodplain appear to be an essential prerequisite for any intact floodplain ecosystem. This will also hold true under changing climatic conditions. Therefore, the maintenance or restoration of functional floodplain areas is of paramount importance.

Zusammenfassung

Auen sind dynamische und produktive Ökosysteme, in denen zahlreiche Pflanzen- und Tierarten vorkommen und die als Hotspot der Artenvielfalt angesehen werden. Die dynamischen Bedingungen in Auen sind insbesondere durch starke Schwankungen in den Wasserständen charakterisiert. So kommt es zu saisonal auftretenden (abhängig vom Abflussregime der Flüsse mehr oder weniger regelmäßigen) Hochwässern und im Sommer oft zu ausgeprägt trockenen Bedingungen. Die hydrologischen Prozesse resultieren in einer großen Strukturvielfalt und einer charakteristischen Vegetationszonierung entlang des Höhengradienten in Auen. Aufgrund der mosaikartig eng beieinanderliegenden Vegetationszonen finden viele Pflanzenarten geeignete Habitate. Auch viele seltene Pflanzenarten, wie die Stromtalpflanzen, kommen in Auen vor, insbesondere in den durch Mahd genutzten Auenwiesen. Allerdings sind artenreiche Auenwiesen in den letzten Jahrzehnten selten geworden, hauptsächlich verursacht durch die Intensivierung der Landnutzung, aber auch durch den Ausbau der Flüsse und den damit einhergehenden Bau von Dämmen und Deichen. Infolgedessen gelten die artenreichen Auenwiesen als naturschutzfachlich wertvoll, werden in bestimmten Ausprägungen nach der FFH-Richtlinie geschützt und stellen mancherorts die Ziel-Pflanzengemeinschaften von Renaturierungen dar.

Der Klimawandel könnte eine weiterhin zunehmende Gefährdung der artenreichen Auenwiesen bewirken. Aufgrund des anthropogenen Klimawandels werden für Mitteleuropa neben höheren Temperaturen trockenere Sommer und längere Trockenphasen für den Zeitraum 2071 bis 2100 projiziert. Abgesehen von den direkten Auswirkungen des veränderten Klimas auf die Standortbedingungen der Auen könnten die Niederschlagsveränderungen in den Einzugsgebieten der Flüsse zu einem veränderten Abflussgeschehen führen und somit die Überflutungsdynamik der angrenzenden Auen beeinflussen. Ob und wie sich der Klimawandel direkt (durch veränderte Temperaturen und Niederschlagsregime) und indirekt (durch veränderte Grundwasserstände) auf die artenreichen Auenwiesen auswirken wird ist derzeit ungewiss.

Das Hauptziel dieser Arbeit war, mögliche Folgen des Klimawandels auf Auenwiesen in Mitteleuropa abzuschätzen. Zu diesem Ziel wurden vier Untersuchungen durchgeführt, die sich mit verschiedenen Aspekten des Themas befassen: (1) dem heutigen Einfluss des Klimas auf die Vegetation der Auenwiesen, (2) den Effekten reduzierter Wasserverfügbarkeit auf die Keimung von Arten des Auengrünlands, (3) den Effekten von reduziertem Sommerniederschlag auf die Menge und Qualität von Heu der Auenwiesen und (4) den Effekten von verschiedenen Wasserständen und Konkurrenz auf die seltene Stromtalpflanze *Cnidium dubium*.

In der ersten Studie wurde untersucht, ob sich ein Einfluss der heutigen Klimabedingungen auf das Auengrünland entlang der Mittelelbe zwischen Bleckede und Wörlitz detektieren lässt (Kapitel 2). Der klimatische Gradient entlang der Mittelelbe ist durch vergleichsweise kontinentale Bedingungen im Südosten und ozeanische Bedingungen im Nordwesten charakterisiert. Wenn es einen feststellbaren direkten Einfluss des derzeitigen Klimas auf die Vegetation von feuchten und frischen Auenwiesen gibt, ist dies ein Indiz dafür, dass sich die Klimaveränderungen auch in der Zukunft auf die Auenvegetation auswirken werden. Insgesamt wurden 46 Vegetationsaufnahmen in feuchten und frischen Auenwiesen von Bleckede bis Wörlitz angefertigt. Die Ergebnisse zeigten Unterschiede in der Artenzusammensetzung in den feuchten Auenwiesen entlang der Mittelelbe (aber nicht in den frischen Wiesen). Dies zeigte sich in Ordinationen, in denen sich die Vegetationsaufnahmen der feuchten Wiesen entsprechend der geografischen Lage entlang der Elbe anordneten. Die „sample scores“ der Ordinationsachsen korrelierten mit klimatischen Parametern wie dem langjährigen mittleren Jahresniederschlag und der langjährigen mittleren Jahrestemperatur. Indikatorarten für die Untersuchungsflächen beider Wiesentypen waren zumeist gewöhnliche Wiesenarten. Der Anteil der Stromtalpflanzen war vergleichsweise ausgeglichen entlang des Gradienten. In frischen Wiesen war die Deckung der Stromtalarten in den westlichen Flächen höher als in den östlichen Flächen. Das Vorkommen typischer Stromtalpflanzen scheint in erster Linie durch hydrologische Faktoren (und die Nutzung) bedingt zu werden. Diese Arten könnten relativ robust gegen die direkte Veränderung von klimatischen Parametern sein. Bei Betrachtung der gesamten Pflanzengemeinschaften deuten die Ergebnisse an, dass es insbesondere im feuchten Grünland aufgrund der projizierten Temperaturerhöhungen im Zuge des Klimawandels zu Veränderungen in den Deckungsverhältnissen der Vegetation kommen könnte. Es muss aber berücksichtigt werden, dass sich die Veränderung des Klimas indirekt über veränderte Abflüsse der Elbe auf alle Arten der Auenvegetation auswirken würde.

Während adulte Pflanzen (in Abhängigkeit von der Lebensdauer) noch vergleichsweise lange unter veränderten Bedingungen an einem Ort ausharren können, reagieren die frühen Lebensphasen von Pflanzen, insbesondere die Keimung, möglicherweise stärker auf veränderte Umweltbedingungen. Die zweite Studie (Kapitel 3) befasst sich daher mit der Frage, wie sich der Klimawandel auf die Samenkeimung von Arten des Auengrünlands auswirken könnte. Dabei wurde auch untersucht, ob sich Arten von trockenen und feuchten Habitaten des Auengrünlands und ob sich an der Elbe und am Rhein gesammelte Samen unterscheiden. Dazu wurden in einem Keimungsexperiment die Samen von 20 Auengrünlandarten (die in ihren Feuchteansprüchen ihrer Habitate differieren) den projizierten trockeneren Bedingungen (Wasserpotentialen von 0 bis -1,5 MPa) bei zwei unterschiedlichen Temperaturregimen (5/15 °C und 10/20 °C) ausgesetzt. Die Samen von fünf der Pflanzenarten wurden an der Elbe und am Rhein gesammelt. Bei Betrachtung aller Arten gemeinsam führte die Reduzierung der Wasserverfügbarkeit zu einer Verringerung der prozentualen Keimung, zu einer abnehmenden Keimungsgeschwindigkeit und zu einer geringeren Synchronität der Keimung (d. h. die zeitliche Streuung der Keimung nahm zu). Zeigerarten für trockene Habitate zeigten eine signifikant niedrigere prozentuale Keimung als Zeigerarten für feuchte Habitate. Die beiden untersuchten Temperaturregime wirkten sich zwar nicht auf die prozentuale Keimung aus, aber auf die Keimungsgeschwindigkeit: Bei geringerer Temperatur war die Keimung schneller. Die Keimung der Samen von Elbe und Rhein unterschied sich nicht. Vermutlich folgen die Feuchte- und Trockenzeiger unterschiedlichen Keimungsstrategien. Während die Samen der Feuchtezeiger eine schnelle und synchrone Keimung aufweisen, da die Wahrscheinlichkeit für geeignete Etablierungsbedingungen in ihrem Habitat hoch ist (Optimisten), weisen die Trockenzeiger eine stärker asynchrone, d.h. zeitlich gestreute Keimung auf, da die Wahrscheinlichkeit für geeignete Etablierungsbedingungen in ihrem Habitat vergleichsweise gering ist (Pessimisten). Der durch den Klimawandel bedingte Rückgang der Sommerniederschläge könnte zum Absinken der Flusswasserstände sowie des Grundwasserspiegels und somit zu trockeneren Bodenbedingungen führen. Eine Folge des Keimungsverhaltens der Feuchtezeiger wäre dann möglicherweise, dass sich die Arten feuchter Standorte aufgrund ihrer schnellen und synchronen Keimung bei zu trockenen Bedingungen nicht erfolgreich etablieren können. Daher scheinen sie für die Folgen des Klimawandels besonders vulnerabel zu sein.

Da Auenwiesen auf regelmäßige Nutzung durch Mahd angewiesen sind, wurde in der dritten Studie untersucht, wie sich die Quantität und Qualität des Heus von Auenwiesen unter den zukünftigen Bedingungen verändern könnte (Kapitel 4). In Feldexperimenten wurden die Effekte von reduzierten Sommerniederschlägen auf die Quantität und Qualität des Heus von Auenwiesen an zwei Elbe-Nebenflüssen (25 % Niederschlagsreduktion von 2009-2011) und am Rhein (25 % und 50 % Niederschlagsreduktion von 2011-2012) untersucht. Als Antwortvariablen wurden die Menge der Biomasse sowie deren Gehalte an Rohfaser, Rohprotein, Energie, Fruktan, Phosphor, Kalium und Stickstoff gemessen sowie der jährliche Ertrag (Biomasse * Energie) bestimmt. Eine Niederschlagsreduktion von 50 % bewirkte eine Reduktion des jährlichen Ertrags am Rhein. Der für die Landwirtschaft besonders wichtige erste Schnitt hat an beiden Flüssen nicht auf die veränderten Bedingungen reagiert (abgesehen von erhöhten Werten an Fruktan bei Niederschlagsreduktion am Rhein). Der zweite Schnitt der Wiesen an den Nebenflüssen der Elbe hat ebenfalls nur schwach auf die experimentelle Behandlung reagiert. Im Gegensatz dazu gab es Effekte der Niederschlagsreduktion um 50 % auf den zweiten Schnitt in den Experimenten am Rhein. Während die Gehalte an Stickstoff und Rohprotein in dem Heu bei Niederschlagsreduktion zunahmen, sanken die Gehalte an Rohfaser bei diesen Bedingungen ebenso wie die Menge der geernteten Biomasse. Dass der erste Schnitt an beiden Flüssen nicht von der Niederschlagsreduktion beeinflusst wurde, hängt vermutlich mit der ausreichenden Wasserversorgung durch die vergleichsweise hohen Wasserstände im Winter und Frühjahr an den Auenstandorten zusammen. Da der erste der für die Landwirtschaft wichtigere Schnitt ist, könnte die Nutzung der Auenwiesen bei moderaten klimatischen Änderungen auch zukünftig tragfähig sein. Diese Einschätzung trifft aber nur zu, solange die Wasserstände der Flüsse im Frühling/ Frühsommer nicht aufgrund des Klimawandels stark absinken.

Neben den direkten klimatischen Änderungen können durch den Klimawandel andere Umweltfaktoren, wie die Grundwasserstände der Auen, durch modifizierte Niederschlagsregime verändert werden. Daher wurden in der vierten Studie die Effekte von Grundwasserstand, Konkurrenz und Herkunft auf die charakteristische Stromtalpflanze *Cnidium dubium* untersucht (Kapitel 5). Zwei Mesokosmen-Experimente wurden durchgeführt, um die Effekte von unterschiedlichen sommerlichen

Grundwasserständen auf *Cnidium dubium* zu untersuchen. In dem ersten Experiment wurden unter gleichen Bedingungen gekeimte Jungpflanzen von *Cnidium dubium* von der Sude und der Havel verschiedenen Wasserständen (20, 40 und 60 cm unter der Topfoberfläche) ausgesetzt. Im folgenden Jahr wurde das Experiment unter Hinzuziehung des Faktors Konkurrenz wiederholt, indem aus Wiesen an der Sude und Havel direkt Soden ausgestochen wurden. Diese Soden enthielten in der Mitte *Cnidium dubium*-Pflanzen und weiterhin die typische Begleitflora der Auenwiesen. *Cnidium dubium* zeigte ohne Konkurrenz bei Wasserständen von 40-60 cm unter der Topfoberfläche das beste Wachstum. Grundwasserstände in diesem Bereich können als physiologisches Optimum dieser Art in Bezug auf diesen Umweltfaktor angesehen werden. Weiterhin konnten Hinweise auf genetische Unterschiede der *Cnidium dubium*-Pflanzen zwischen den Populationen der zwei Herkünfte gefunden werden, da die *Cnidium dubium* Pflanzen von der Havel über den Verlauf des gesamten Experiments längere Blätter aufwiesen als die Pflanzen von der Sude. Unter Konkurrenzbedingungen wurden jeweils bei dem Wasserstand die längsten Blätter von *Cnidium dubium* gebildet, bei dem die Konkurrenzintensität am höchsten war. *Cnidium dubium* konnte also bei allen drei getesteten Wasserständen das Wachstum den Konkurrenzbedingungen anpassen. Somit kann davon ausgegangen werden, dass sich sommerliche Grundwasserstände in diesem Bereich (20-60 cm unter Flur) eignen, um artenreiche Auenwiesen, zumindest die charakteristische Auenwiesenart *Cnidium dubium* zu fördern.

Insgesamt legen die Ergebnisse der vorliegenden Arbeit nahe, dass sich die veränderten Grundwasserstände in der Aue (durch die veränderten Abflüsse der Flüsse) stärker auf die Vegetation des Auengrünlands auswirken werden als die direkten klimatischen Veränderungen. Im Hinblick auf die zwei untersuchten Vegetationstypen von Auengrünland, die feuchten und frischen Wiesen, müssen die feuchten Wiesen als vulnerabler im Vergleich zu den frischen Wiesen für die Effekte des Klimawandels angesehen werden.

Wenn eine zunehmende Trockenheit, die gegen Ende des 21. Jahrhunderts durch die geringeren Niederschläge im Sommer ausgelöst werden könnte, tatsächlich eintritt, könnten Managementstrategien zur Förderung der seltenen Stromtalarten notwendig werden. Den Grundwasserstand im Sommer auf 20 cm bis 60 cm unter Geländeoberfläche zu erhöhen wäre vermutlich eine geeignete Maßnahme, um Trockenstress zu vermeiden und artenreiche Auenwiesen zu fördern. Der Erhalt der dynamischen, d.h. jahreszeitlich schwankenden hydrologischen Bedingungen erscheint neben der Aufrechterhaltung einer geeigneten Landnutzung der rezenten Aue die wichtigste Bedingung für den Schutz der charakteristischen Auenwiesenarten zu sein.

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Last but certainly not least, bedanke ich mich bei meinem Freund Harry. Danke für Deine Liebe und Geduld und das immerwährende Interesse an meiner Arbeit. Und ach ja, danke für das gemeinsame Markieren der Untersuchungsplots an Sude und Havel, für das Ertüfteln einer Niederschlagsreduktionsdachentwässerung (das ist vermutlich das längste Wort dieser Arbeit) und die Hilfe bei der Biomasseernte.

Outline of the author´s contributions

The four manuscripts of this thesis have all been submitted to peer-reviewed international scientific journals. Three manuscripts are already published (Chapter 2, 3 and 5) and one is submitted (Chapter 4). The author of this thesis contributed to the chapters as follows:

- Writing the introduction (chapter 1) and the synthesis (chapter 6).
- Writing the manuscripts for chapters 2, 3 and 4. Jana Melanie Hanke and the author of this thesis contributed equally to writing of chapter 5.
- Data analysis for chapters 2, 3 and 4. Jana Melanie Hanke and the author of this thesis contributed equally to the data analysis of chapter 5.
- Preparing all figures and tables for chapters 2, 3 and 4.
- Sampling and processing the samples from the Elbe experiments for chapter 4 and from the water level experiment witout competition for chapter 5.
- Conception and design of the studies for chapters 2, 4 and 5.

List of photographs

All photographs throughout this thesis were taken by Kristin Ludewig except otherwise indicated in the following list. The photographs of the same page are always listed from the left to the right side of the page.

Page	Image
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iv	Floodplain at the Elbe River
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1	*Stellaria palustris*
1	*Succisa pratensis*
12	Floodplain at the Elbe River
13	Measuring elevation with a Trimble GPS
13	*Carduus nutans* in the Elbe River floodplain
13	Coming to unify the estimation of plant abundances between estimators
34	Seedling of *Cnidium dubium* in the Havel River floodplain
35	*Centaurea jacea*
35	Petri dishes of the germination study (by Bianka Zelle)
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57	Precipitation reduction experiment at the Rhine River
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78	Water level experiment with *Cnidium dubium* without competition
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79	Me with a sod including *Cnidium dubium* (by Jana M. Hanke)
96	Floodplain at the Havel River
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97	Small summer flooding 2010 at the Sude
97	Spring flooding at the Elbe River
126	Having help from Joachim Osterburg and my father

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Re: Dissertation written by Kristin Ludewig

To whom it may concern,

As a native English speaker and experienced proofreader, I hereby confirm that the abovementioned dissertation “Possible effects of climate change on the vegetation of floodplain meadows" has been written in correct and concise English.

Kind regards

Ian Bennett

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und ausschließlich die angegebene Quellen und Hilfsmittel verwendet habe.

Hamburg, den 09.09.2014 Kristin Ludewig