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Conservation on the edge: habitat conditions and management strategies to maintain amphibious plant communities of temporarily flooded field ponds in north-east Germany

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Summary

Thousands of years of historical farming practices formed a highly adapted arable flora that declined during the past decades due to an ongoing intensification of agricultural management. To preserve arable biodiversity, research has focused mainly on terrestrial plant communities, resulting in the implementation of a variety of tools and conservation programmes. Amphibious plant species, many of them rare and threatened, and their communities inhabiting temporarily flooded parts of arable fields have been less well investigated. Therefore, this dissertation aims at studying the effects of water level fluctuations and agricultural management on this species group in order to develop a conservation concept for plant communities at temporarily flooded habitats in arable fields.

In a first field study the effects of water level fluctuations, soil properties and agricultural management on the vascular plant communities were examined. The main findings show that fluctuating water levels increased total species richness and the proportion of species belonging to the dwarf rush communities (phytosociological class Isoëto-Nanojuncetea bufonii Br.Bl. et R.Tx. 1943), which harbours many rare amphibious plant species. The species composition was mainly determined by the water regime, whereas soil fertility had a subordinate impact. The effects of farming practices on diversity and species composition were less clear. These results indicate that supporting fluctuation of water levels and keeping the soil nutrient content low would best promote amphibious plant communities in arable fields.

As plant species at disturbed habitats like temporary ponds produce persistent seeds, the soil seed bank plays an important role for the conservation of amphibious plant communities. At temporarily flooded depressions, both terrestrial and amphibious plant species contribute to the seed bank, which in turn may harbour the potential for a series of alternating, valuable plant communities. To get a better understanding, how the hydro-period and depth of the water table determine diversity, species composition and conservation value of these communities, a common garden

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experiment was conducted. Mixed soil samples of the upper and lower littoral zone were kept flooded for short, intermediate or long time periods at differing depths (5, 15, 40 cm) and diversity, number of rare species and species composition of the emerging seedling communities were evaluated. In general, hydro-period most decisively changed species composition and diversity. In all treatments, few rare species emerged, but species composition differed, indicating that all communities along the flooding gradient harbour species of high conservation value. Thus, these findings show that the seed bank has the potential for the conservation of different plant communities in fluctuating ecosystems.

Apart from environmental factors like water level fluctuations, the agricultural land use is of great importance for maintaining plant communities in arable fields. Intensified farming practices have led to severe declines of arable plant diversity at terrestrial sites. However, studies on the effects of farming practices like soil tillage, crop competition, fertilization and herbicide application, and their respective combinations on population dynamics of amphibious plant species inhabiting temporarily flooded fields are scarce. Considering the high conservation value of amphibious plant communities, it is highly desirable to understand these processes, in order to develop efficient conservation strategies. Thus, the third main chapter of this dissertation comprises an on-farm experiment with four selected amphibious plant species (Elatine alsinastrum, Limosella aquatica, Myosurus minimus, Peplis portula), where aboveground plant establishment and belowground seed densities were determined. The plant emergence of all study species was reduced by herbicide application, whereas soil tillage positively affected the establishment in the field. Plant densities were controlled by fertilizer and herbicide application, with pronounced effects on Limosella aquatica and Myosurus minimus. Soil tillage decreased seed densities of Elatine alsinastrum and Peplis portula, while other management practices had marginal effects on the soil seed bank. These findings indicate that reduction of management operations would best promote amphibious plant populations.

The comprehensive approach of the three studies presented in this dissertation, combining an observational field study, a common garden experiment with more

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controlled conditions and an on-farm experiment allowed getting a better understanding of the effects of environmental conditions and agricultural land use on amphibious plant species and their communities. By combining the findings into a conservation concept with management implications for conservation practitioners and farmers, it is possible to take steps toward maintaining this species group in arable fields. Thus, the findings of this dissertation contribute to the conservation of arable biodiversity and can have immediate application in nature conservation projects.

Zusammenfassung

Jahrtausende historischer Ackernutzung haben eine hochangepasste Ackerbegleitflora hervorgebracht, die in den letzten Jahrzehnten durch die fortschreitende Intensivierung der landwirtschaftlichen Nutzung zurückgegangen ist. Zur Erhaltung der Agrobiodiversität hat sich die Forschung bisher vor allem auf terrestrische Pflanzengemeinschaften konzentriert, was in der Implementierung verschiedener Tools und Schutzprogramme mündete. Amphibische Pflanzenarten und deren Artengemeinschaften, von denen viele selten und gefährdet sind, sind dagegen bisher weniger gut untersucht. Diese Dissertation hat daher zum Ziel, die Auswirkungen von Wasserstandsschwankungen und landwirtschaftlicher Nutzung auf diese Artengruppe zu untersuchen, um ein Schutzkonzept für die Pflanzengesellschaften temporär überfluteter Habitate in Äckern zu entwickeln.

In einer ersten Feldstudie wurden die Effekte von Wasserstandsschwankungen, Bodeneigenschaften und landwirtschaftlicher Nutzung auf die Gefäßpflanzengesellschaften untersucht. Die zentralen Ergebnisse zeigen, dass schwankende Wasserstände die Gesamtartenzahl und den Anteil an Zwergbinsenarten deutlich erhöhen. Die Klasse der Zwergbinsengesellschaften (Isoëto-Nanojuncetea bufonii Br.Bl. et R.Tx. 1943) weist eine Vielzahl seltener Arten auf. Die Artenzusammensetzung wurde Wesentlichen durch das Wasserregime ebenso im bestimmt, während Bodenfruchtbarkeit eine untergeordnete Rolle spielte. Landwirtschaftliche Nutzung hatte weniger deutliche Auswirkungen auf Diversität und Artenzusammensetzung. Diese Ergebnisse zeigen, dass durch ein Management, das fluktuierende Wasserstände ermöglicht und den Bodennährstoffgehalt niedrig hält, amphibische Pflanzengemeinschaften in Äckern begünstigt werden.

Da Pflanzenarten gestörter Standorte, wie z.B. temporärer Gewässer, persistente Samen produzieren, kann die Samenbank im Boden möglicherweise eine wichtige Rolle für den Schutz amphibischer Pflanzengemeinschaften spielen. An temporär überfluteten Senken tragen sowohl terrestrische, als auch amphibische Pflanzenarten

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zur Samenbank bei, welche dann das Potenzial für eine Reihe alternierender, wertvoller Pflanzengesellschaften bergen kann. Um besser zu verstehen, wie Überflutungsdauer und Tiefe des Wasserspiegels den Artenreichtum und -zusammensetzung beeinflussen, wurde ein Common-Garden-Experiment durchgeführt. Gemischte Bodenproben der oberen und unteren Uferzone wurden unterschiedlich tief (5, 15, 40 cm) für kurze, mittlere oder lange Perioden überstaut und die Diversität, Anzahl seltener Arten sowie Artenzusammensetzung der Keimlingsgemeinschaften bestimmt. Dabei veränderte die Überstaudauer maßgeblich die Artenzusammensetzung und Diversität. In allen Behandlungen lag die Anzahl aufgelaufener seltener Arten niedrig, jedoch mit unterschiedlicher Artenzusammensetzung, was darauf hindeutet, dass alle Pflanzengemeinschaften entlang des Überflutungsgradienten Arten mit hohem Naturschutzwert enthalten. Folglich zeigen die Ergebnisse, dass die Samenbank das Potenzial zum Schutz verschiedener Pflanzengemeinschaften in fluktuierenden Ökosystemen besitzt.

Abgesehen von Umweltfaktoren, wie den Wasserstandsschwankungen, ist die landwirtschaftliche Nutzung von großer Bedeutung für den Erhalt einer diversen Ackerwildkrautflora. Intensivierte Landnutzung hat zu starken Rückgängen der Ackerwildkrautflora auf terrestrischen Standorten geführt. Für die amphibischen Pflanzenarten temporär überfluteter Ackerstandorte ist dagegen noch kaum bekannt, wie landwirtschaftliche Nutzung, d.h. Bodenbearbeitung, Konkurrenz durch Kulturpflanzen, Düngung und Herbizideinsatz, sowie deren Kombinationen auf die Populationsdynamik dieser Arten wirkt. Das letzte Kapitel umfasst daher einen On-Farm-Bewirtschaftungsversuch mit vier Arten (Elatine alsinastrum, Limosella aquatica, Myosurus minimus, Peplis portula), für die die oberirdische Etablierung und die unterirdischen Samendichten bestimmt wurden. Der Feldaufgang aller untersuchten Arten wurde durch Herbizidanwendung reduziert, während sich Bodenbearbeitung positiv auf die Etablierung auswirkte. Die Pflanzendichten wurden durch Düngung und Herbizideinsatz reguliert, mit deutlichen Effekten bei Limosella aquatica und Myosurus minimus. Bodenbearbeitung reduzierte die Samendichten von Elatine alsinastrum und Peplis portula, wohingegen die anderen Bewirtschaftungsmaßnahmen nur geringe

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Auswirkungen auf die Samenbank hatten. Diese Ergebnisse weisen darauf hin, dass reduzierte Bewirtschaftungsmaßnahmen die Populationen amphibischer Pflanzenarten am stärksten begünstigen würden.

Der komplementäre Ansatz der drei Studien dieser Dissertation, d.h. eine Feldstudie, ein Common-Garden-Experiment unter kontrollierten Bedingungen und ein On-Farm-Versuch, ermöglicht es, ein besseres Verständnis der Auswirkungen von Umweltbedingungen und landwirtschaftlicher Nutzung auf amphibische Pflanzenarten und deren Artengemeinschaften zu bekommen. Wenn die Ergebnisse in einem Schutzkonzept kombiniert werden, das Managementvorschläge für Naturschützer und Landwirte enthält, ist es möglich, Maßnahmen zum Erhalt dieser Artengruppe in Äckern zu ergreifen. Daher tragen die Resultate dieser Dissertation zum Schutz der Agrobiodiversität bei und können unmittelbare Anwendung in Naturschutzprojekten finden.

Chapter 1

General Introduction

Background: Formation and decline of amphibious plant communities at temporarily flooded field ponds

Since the beginning of agriculture a specialized flora developed on arable fields, which was adapted to traditional farming practices (e.g. Burrichter et al., 1993; Fried et al., 2008; Pinke et al., 2012). The close relationship between arable plant community and regularly recurring management operations makes the vegetation of arable land particularly vulnerable to management changes and agricultural intensification (Storkey et al., 2010; Takács et al., 2013). Since the past century the agriculture in many parts of the world has experienced enormous changes in all parts of the crop production process (Kiritani, 2000; van Zanten et al., 2014). Site melioration activities like liming have reduced the heterogeneity of soil properties (Albrecht and Auerswald, 2003). Use of mineral fertilizer has increased competition between crops and arable plants, and application of herbicides has caused a declining diversity of arable plants (Shibayama, 2001; Nie et al., 2009). Land consolidation activities have led to increased field sizes, often going along with a loss of small habitat elements (Tscharntke et al., 2005). Less productive marginal land has been set aside and often converted to grassland, forests or to bioenergy plantations (Falcucci et al., 2007; Bucała, 2014; Hauk et al., 2014). Special crops like lentils, millet, tobacco and flax have become less attractive for farmers, and together with these crops their related arable plant communities have disappeared (Mirek, 1997). Simplification of crop rotations, e.g. the conversion to winter annual rotations or double-cropping have been detrimental for the reproduction success of arable plants (Bambaradeniya and Amerasinghe, 2003; Fachagentur Nachwachsende Rohstoffe, 2010). Enhanced seed cleaning techniques and higher crop densities currently prevent arable plant species from a successful establishment. The latest technological developments like precision farming, no-tillage

management and bioenergy crops with an even higher crop density have reduced most of the remaining biodiversity on arable land (Meyer *et al.*, 2014; Scursoni *et al.*, 2014). All these changes have led to an increased productivity and to a decline in site variability resulting in dramatic losses of arable biodiversity (Albrecht, 1995; Sutcliffe and Kay, 2000; Baessler and Klotz, 2006; Meyer *et al.*, 2013).

The accelerated decline of agro-biodiversity, especially after World War II, raised the attention of ecologists. Numerous studies examined the effects of intensified land use on agro-biodiversity in order to develop effective management strategies for the conservation of arable plant communities (e.g. Tüxen, 1962; Hilbig, 1987; Albrecht, 1995; Baessler and Klotz, 2006; Storkey et al., 2012). An increasing awareness of negative impacts due to intensifying land and resource use resulted in declaring to stop the decline of biodiversity as a political goal (Convention on Biological Diversity 1992). For the conservation of arable biodiversity, first programmes and tools were field flora reserves (Schlenker and Schill, 1979) and the field-margin-program that aimed at reducing fertilizer and herbicide input at field boundaries to maintain rare species there (Schumacher, 1980; Marshall and Moonen, 2002; Walker et al., 2007). Later on, tools like 'Production Integrated Compensatory Measures' (Litterski et al., 2008), or special conservation programmes, e.g. '100 fields for biodiversity' (Meyer et al., 2010) and 'High Nature Value Farmland' (PAN et al., 2011), were established. Within the European agricultural policy, agri-environmental schemes are one important instrument to preserve biodiversity on arable land (European Commission, 1992). However, most of the research on arable conservation, as well as the implemented management strategies focused mainly on arable plants and communities of terrestrial habitats, whereas the species and communities of temporarily flooded parts in arable fields have not been studied well. Only some studies focused on the plant communities in this habitat type (e.g. Jage, 1973; Albrecht, 1999; Hoffmann et al., 2000; Bissels et al., 2005) and few proposed conservation strategies for plant and amphibian communities inhabiting these habitats (Dürr et al., 1999; Berger et al., 2003; Berger and Pfeffer, 2011).

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Formation	Location	Terms	References
(A) Natural habitats Glaciation processes: Dead ice blocks leaving local depressions after melting	North America, northern and central Europe	Potholes, kettle holes	Kalettka (1996); van der Valk (2005)
<i>Climatic conditions:</i> Unevenly distributed precipitation during cold season and hot and dry summers	Semi-arid and arid regions, esp. in mediterranean regions	Temporary ponds, vernal pools, cupular ponds, temporary rivers, ephemeral wetlands	Zacharias and Zamparas (2010); Zacharias <i>et al.</i> (2007); Datry <i>et al.</i> (2011)
Sedimentation processes: Redirection of the riverbed, leading to disconnection of parts of the river	Globally	Oxbow lakes, floodplain backwaters	Abernethy and Wilby (1999); Gallardo <i>et al</i> . (2012)
<i>Tide:</i> Water level fluctuations	Coastal systems	Rock pools, dune lakes	Wones and Larson (1991); Vanschoenwinkel <i>et al.</i> (2009)
(B) Man-made habitats			
Intended: Excavation for watering purposes; fish production, rice production	Globally	Farmland ponds, fish ponds, rice fields	Pinke <i>et al.</i> (2014); Declerck <i>et al.</i> (2006) Koch <i>et al.</i> (2005)
Unintended: Extraction of geological resources, pig pastures	North America, northern and central Europe	Marl pits, clay pits, gravel pits, pig pastures	Day <i>et al.</i> (1982); Pulido-Bosch <i>et al.</i> (2000) Täuber (2000)

Box 1: Overview over different types of temporary ponds, their origins, where these are known from and different terms used in the literature with key references.

Temporary water bodies are small, endorheic wetlands with areas <10 ha (Ramsar definition; Ramsar Convention Secretariat, 2010). They can be found throughout the globe in different climates and environmental conditions (see Box 1). A good review about habitats, their characteristics and vegetation of temporary wetlands on a global perspective can be found in Deil (2005), whereas van der Valk (2012) gives a more

general overview about the biology of freshwater wetlands. In the mediterranean regions, for example, high temperatures together with seasonally distributed precipitation led to the formation of a special, protected habitat type, the mediterranean temporary ponds that are a priority habitat under the Natura 2000 network of the European Union (Natura code: 3170, Habitats Directive 92/43/EC). In more humid, temperate climates, natural temporary wetlands can be found, as well. Glaciation during the Ice Ages left ice blocks that formed small local depressions after melting, so called kettle holes or potholes. In landscapes that were influenced by the Ice Ages, high densities of these wetlands can be found, like in the prairie pothole region in North America or in the younger moraine landscape of north-east Germany, where their number exceeds 150,000 (Bluemle, 2000; Kalettka and Rudat, 2006; Mitsch and Gosselink, 2007). Apart from the influence of glaciation processes, deforestation during and after the Medieval Age forced the formation of water logging soil layers, which induced a groundwater rise and increased the number of temporarily flooded depressions in various parts of Europe (Klafs *et al.*, 1973).

In spite of their small area, ponds contribute significantly to the local and regional species richness and often harbour high numbers of rare species (Dreger, 2002; Oertli *et al.*, 2002; Williams *et al.*, 2004; Biggs *et al.*, 2007; Davies *et al.*, 2008). Thus, some authors regard them as biodiversity hotspots (Kalettka *et al.*, 2001; Cereghino *et al.*, 2014). Scheffer *et al.* (2006) hypothesize that the absence of fish in small water bodies increases the likelihood of the wetland to be in a vegetated state, for which several studies could show that this promotes a high biodiversity of most trophic groups (Jeppesen *et al.*, 1997; Scheffer, 2004). A great heterogeneity among ponds in terms of chemical soil and water properties, as well as differences in shape, slope and depth provides various microsites which may support a high beta diversity (Lischeid and Kalettka, 2012). This assumption is supported by Oertli *et al.* (2002), who showed that many small ponds harbour a higher biodiversity and more rare species than one big pond with the same total area. However, they also found that species inhabiting the big pond were missing in the small ponds, and therefore, conservation strategies should aim at maintaining and protecting ponds with different sizes. Besides amphibious plant

species, also invertebrates show higher numbers of rare species in ponds than in other freshwater habitats within agricultural landscapes (Biggs *et al.*, 2007).

On a global scale, the total area of ponds (permanent and temporary ponds) covers approximately 30 % of the global surface area of standing waters (Downing *et al.*, 2006), which is more than the area of larger standing freshwater wetlands, including lakes. Several studies reported that ponds occur in high numbers throughout Europe and in some regions they even exceed the number of lakes by more than 100 times (Switzerland; see EPCN, 2008) or make up more than 95 % of the standing waters (Great Britain; see Biggs *et al.*, 2005), showing their great importance for protection of aquatic biodiversity (Biggs *et al.*, 2005; Søndergaard *et al.*, 2005; EPCN, 2008). Unfortunately, land-use intensification has led to severe declines in pond numbers.

Throughout Europe, temporary water bodies have decreased, in some regions by more than 50 % (Weinreich and Musters, 1989; Kalettka, 1996; Boothby and Hull, 1997). In many parts of the Federal State of Brandenburg in Germany, for example, the number of kettle holes and temporarily flooded depressions considerably decreased due to land consolidation and melioration during the 1950s (Kalettka, 1996; Kalettka et al., 2001). Beside melioration, nutrient and pesticide input are further threats to pond biodiversity (Boothby, 2003). Due to their small catchment areas, ponds are particularly sensitive to eutrophication and pollution. However, since many ponds have been always nutrient sinks with a high trophic level, eutrophication must not necessarily impact the local pond biodiversity and depends much on the taxonomic group studied (Rosset et al., 2014). However, as extensive eutrophication in a pond landscape can negatively affect the regional biodiversity, different trophic levels should be maintained to keep varying living conditions there. Other authors, like Declerck et al. (2006), found that the proportion of cropland area surrounding ponds in an English agricultural landscape to be negatively correlated to the ecological quality of the ponds, highlighting the importance of improved management strategies to maintain biodiversity within landscapes under intensive agricultural land use.

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Agricultural land use determines species occurrence

Two main factors determine the living conditions of temporarily flooded depressions in arable fields. Similar to other agricultural habitats, the land-use practices determine which species are able to establish and contribute to the plant communities emerging. Soil tillage is performed to reduce competition between crops and arable plants. On the one hand, seeds of arable plants, buried to deeper soil layers fail to germinate (Froud-Williams *et al.*, 1984; Scopel *et al.*, 1994; Baskin and Baskin, 2014) and thus, the seed bank of competing weeds is reduced. At the other hand, established plants are uprooted and competition is reduced, as well. Timing of tillage that is mainly determined by the sown crop, leads to the selection of different species (Lososová *et al.*, 2004). In winter-sown crops, winter annual species are promoted, as they are able to germinate after soil tillage in autumn, when crop cover is still low.

Herbicide application is used in conventional agriculture to reduce competition between crops and weeds during the growth phase of the crops (Proctor, 1986; Shelke, 1987). The application timing determines, which arable plant species are reduced. Application in autumn and early spring leads to the reduction of winter annual species, whereas summer annuals are not affected (Albrecht, 1989). Additionally, the type of herbicides used and doses can change the effects on the weed species (Rotches-Ribalta *et al.*, 2015). Broad-spectrum herbicides reduce all weeds, whereas more specific herbicides, like types that control broad-leaf weeds, can indirectly promote grass species and vice versa.

The sown crop has major indirect effects on the population and species composition of arable weeds (Lososová *et al.*, 2004), as it determines the intensity and timing of all other farming practices. Additionally, the row space and height of the crops lead to changes in crop cover and density (Weiner *et al.*, 2001) and thus, the light availability for germinating seeds at the soil surface (Epperlein *et al.*, 2014). Accordingly, winter annual weed species are promoted in winter-sown crops, as the light availability and competition with the crop is still low in autumn and early spring. Contrastingly, in late spring the crop cover of winter sown crops can be already high and limit the germination of summer annuals.

Fertilization in general, promotes growth and reproduction success of most plant species. In competition with other species, it promotes competitive species with a high nutrient-use efficiency, which in turn suppresses less competitive and low growing species (Whigham, 1984; Kleijn and van der Voort, 1997; Storkey *et al.*, 2010).

Environmental factors: water regime has the main impact

Apart from the land use practices, environmental factors affect the occurrence of species at temporary water bodies. Among these factors, hydro-period, the depth of the water table, and the timing of flooding are most important (e.g. Casanova and Brock, 2000). Kneitel (2014) showed that the timing of flooding results in different plant communities. The hydro-period and the water level are determined by the size of the catchment area, the slope, the soil substrate and the climatic conditions. Since temporary ponds usually don't have an inflow or outflow, water level and hydro-period are determined by precipitation and/ or the groundwater regime (Pitchford et al., 2012). In wetlands disconnected to the groundwater table, the catchment area determines the amount of water that enters the wetland and, together with the slope it defines the average and maximum height of the water table. The soil substrate regulates how fast the water can infiltrate the soil and it also affects the rate of evaporation (Blume et al., 2010). Additionally, the water regime of ponds is strongly influenced by the weather conditions. Thus, high temperatures in combinations with intense sunshine, as well as high wind speed lead to high evapo-transpiration rates (Mitsch and Gosselink, 2007). The seasonal distribution and amount of precipitation is also important. During years with precipitation above the long-term mean, the depressions fill and the number of flooded ponds increases, whereas years with precipitation below the long-term average precipitation lead to reduced numbers of flooded depressions (Schmidt, 1996).

Species characteristics: Adaptations to survive in fluctuating ecosystems

Like many terrestrial arable plants, most amphibious plant species are 'ruderal' species sensu Grime (1979) with a short life cycle, producing large amounts of persistent seeds that are dispersed by wind, water or with soil attached to feet of animals or agricultural machinery (Salisbury, 1970). In temporary water bodies, water level fluctuations, their timing, frequency and duration determine which species are able to germinate and establish (von Lampe, 1996; Casanova and Brock, 2000). Many amphibious plant species are able to germinate under flooded conditions (von Lampe, 1996; Poschlod et al., 1999). Timing and duration of inundation lead to different conditions of oxygen availability and temperature, each of them can inhibit or promote germination, depending on species-specific requirements (Kennedy et al., 1980; Matsuo et al., 1984). Due to the high thermal capacity of water, the depth of the water body considerably modifies the microclimatic conditions at the bottom. High water columns buffer the amplitude of temperature changes between day and night, which is an important signal for the germination of many amphibious plants (Pons and Schröder, 1986). Light intensity is reduced with increasing water depth, also reducing the germination of various species (Baskin and Baskin, 2014). To adapt to the variable hydrological conditions, many amphibious plant species are able to respond to flooding morphologically. They can develop different leaf and stem forms as well as differentiated tissues, which enable them to grow under both flooded and terrestrial site conditions. Brock and Casanova (1997) developed a system of plant functional types to categorize these species according to their ability to morphologically respond to flooding without being harmed. They distinguish between submerged plants, amphibious plant species that can respond morphologically to flooding or tolerate flooding, and terrestrial species that cannot tolerate flooding. All these factors together lead to differences in the establishing plant communities (Keddy and Ellis, 1985; Hoffmann, 1996; von Lampe, 1996; Casanova and Brock, 2000). Figure 1 displays how differences in flooding and farming intensity lead to a vegetation zonation along a hydrological gradient at the littoral zone of wetlands.



Figure 1: Zonation of the littoral zone at a field pond along a hydrological and soil texture gradient from the permanently aquatic area at the left side of the graph to the area permanently under agricultural use at the right hand side. Plant functional types, vegetation structure, relief and soil texture are shown in the diagram, hydrology and land use are explained in the text. Adapted from Hoffmann (1996).

Objective: Developing a concept for the conservation of threatened amphibious plant communities

As amphibious plant species are highly adapted to the specific living conditions at temporarily flooded ponds, they are particularly vulnerable to the environmental and agricultural land use changes that this habitat type experienced during the past century. Thus, many species of amphibious plant communities are considered threatened and rare (Ludwig and Schnittler, 1996).

This dissertation aims to develop a concept for the conservation of the amphibious plant communities of temporarily flooded parts of arable fields. Thus, it is important to understand the impact of environmental conditions and agricultural management practices on these species and communities. The dissertation consists of three parts that account in different approaches for these factors (Figure 2). In a first descriptive field study both, the effects of water level fluctuations and farming practices on the diversity and species composition of the apparent vegetation at temporarily flooded field ponds were studied. To get a more detailed understanding of the effects of water level fluctuations and the related options for conservation management, a common garden experiment was used in the second chapter. Finally, the effects of agricultural management practices were tested in an on-farm experiment at the population level for selected species.

	Chapter 2			D	escriptive field study	
	Effects on diversity species composition	and า				
	Enviro	onmental factors	&	Agricultural lar	nd use	
	Conservation value communities	of potential		Effects on popu field and the so selected specie	ulation dynamics in th bil seed bank of es	ne
С	hapter 3	Common garden experiment		Chapter 4	On-farm experime	ent
[Conservatio management r	n co recc	oncept with		

Figure 2: Conceptual diagram of the three dissertation chapters.

The main factors changing establishment and reproduction success of the amphibious plant species are given in bold.

Outline

Chapter 2 'Effects of water regime and agricultural land use on diversity and species composition of vascular plants inhabiting temporary ponds in northeastern Germany' deals with the question, how water level fluctuations and soil properties as environmental factors and agricultural land use determine the diversity and species composition of amphibious plant communities at temporarily flooded field ponds. The vegetation composition was examined at different ponds under different water regimes and management practices at one farm. This chapter serves as an overview to examine the factors structuring the plant communities inhabiting temporary ponds in the study area, in order to get a basis for the development of efficient conservation strategies.

Chapter 3 'Managing plant species diversity under fluctuating site conditions – the case of temporarily flooded depressions' focuses on the effects of water level fluctuations on diversity and conservation value of amphibious plant communities. To study the effects of the water regime under more controlled conditions, a flooding experiment was conducted with seed bank samples from the upper and lower littoral zones that were cultivated under a series of different hydro-periods and water levels. As we could show that the soil seed bank of temporary ponds can harbour the potential for a series of alternating plant communities, all with a high conservation values, this study also highlights the potential for conserving different plant communities in fluctuating ecosystems.

Chapter 4 'Effects of farming practice on populations of threatened amphibious plant species in temporarily flooded arable fields – implications for conservation management' deals with the effects of agricultural land use on the population dynamics of four threatened study species. In an on-farm experiment the plant densities of the studied species in the field as well as their seed densities in the soil seed bank were examined before, during and two years after the establishment of field plots with or without the following treatments in pure application or combination: soil tillage, sowing crops, fertilization and herbicide input. The resulting effects on the populations of the study species are presented and it is discussed, how a sophisticated

management of temporarily flooded parts in arable fields could help to conserve amphibious plant populations and their communities.

Combining approaches to assess site factors, soil seed bank and consequences of management create a better understanding of the interactions between land use, environmental conditions and species and can ultimately lead to the development of a conservation strategy and management implications.

Study site

The studies, described in Chapters 2 and 4, were carried out on one conventionally managed farm in the Federal State of Brandenburg (80 km northeast of Berlin; 55 m a.s.l.; N52°55', E14°02'). The seed bank samples, used for the flooding experiment in Chapter 3, were collected at temporarily flooded depressions on the same farm. Northeast Brandenburg is part of a younger moraine landscape, formed during the last Ice Age (Weichsel). During the Medieval Age extensive forest clearances have led to rising ground water levels that in turn, led to the flooding of local depressions, where layers of clay in the soil inhibited the infiltration of water (Klafs et al., 1973). Accordingly, high numbers of kettle holes and so called pseudo-kettle holes can be found in the study area (Kalettka, 1996). Especially the variation in precipitation above and below the long-term mean lead to the characteristic water level fluctuations among years (Schmidt, 1996). The soils in the study area can be characterized as fertile Luvisols, according to the German soil classification system 'Parabraunerde' with a pH of approximately 6.8 (own data) consisting of sandy loam or loamy sand (MLUV and Stiftung NaturSchutzFonds Brandenburg, 2005a). In temporarily flooded depressions Stagnosols ('Pseudogleye') and in more permanently flooded parts also Histosols ('Erdund Mulmmoore') can be found (MLUV and Stiftung NaturSchutzFonds Brandenburg, 2005b).

The climatic conditions of the study site (more detailed information and map see Chapter 2) are characterized by a temperate climate with a mean annual temperature of 9 °C and 500 mm of precipitation, with the lowest temperatures in January (average of 0 °C) and highest temperatures in July (average of 18.5 °C). Precipitation is unevenly distributed with highest averages of 61 mm in July and lowest averages of 30 mm in February (long-term mean from 1981–2010; DWD, 2014).

Study species

References for the descriptions: Hegi (1925, 1926); Hartl and Wagenitz (1965); Conert *et al.* (1974); and Jäger (2011). Dispersal and seed longevity information were obtained from the LEDA traitbase (Kleyer *et al.*, 2008). For the results of seed and capsule counting see Appendix A1.

Elatine alsinastrum L. is a small species of the family Elatinaceae that can reach plant heights from 2–50 cm. Depending on the water level, the species develops a terrestrial or an aquatic form with ascending (terrestrial) or erect (aquatic) stems that can have branches at the base. The sessile leaves are arranged in whorls. Under submerged conditions the internodes are elongated, with at least eight lineal leaves per whorl. Above the water surface whorls usually have three to eight ovoid to lanceolate leaves. The greenish flowers are arranged in the leaf axils of emergent or terrestrial leaves. The oblong, cylindrical and slightly curved seeds are released soon after ripening. The time of flowering ranges from June to September. The species is distributed throughout Europe and Siberia (Popiela *et al.*, 2013). According to own counts, the species can have between 3–37 capsules with an average of 42 seeds per capsule. The thousand-seed weight is around 15 mg. According to the LEDA traitbase, *Elatine alsinastrum* develops a transient seed bank. There is no information about the way the seeds of this species are dispersed, but it can be assumed that like the other species, seeds are dispersed via water and with soil attached to the feet of animals.

Limosella aquatica L., a stoloniferous species of the family Scrophulariaceae, forms rosettes with diameters ranging from 2–8 cm. The leaves have long petioles and lanceolate to ovoid shaped laminae. Leaves from submerged plants reaching the water surface form floating leaves with a more ovoid shape, whereas in greater depths submerged leafs are awl-shaped. The small, rosy or white flowers appear at the base of the rosettes (see Box 2). *Limosella aquatica* flowers from June to October and produces between 5–233 capsules with a mean of 68.5 seeds per capsule, according to own counts. The seeds have on average a thousand-seed weight of 14 mg. The short-term persistent seeds are released shortly after ripening and are dispersed via water or attached to the feet of animals. It has a widespread distribution, mainly at the northern

hemisphere, in Europe, Asia and North America. According to Brock and Casanova (1997), the species can be regarded as an 'amphibious fluctuation responder'.

Myosurus minimus L. is a species within the family Ranunculaceae, with lineal leaves forming rosettes with heights ranging from 2–10 cm. The greenish flowers appear on an elongated stem with one flower per stem. The up to 6 cm long, mouse-tail like infructescence bears the nuthlets, with 100–400 seeds per infructescence and thousand-seed weight of 139 mg. The winter annual species flowers in early spring from April to June and seeds are dispersed by seed contamination, by water or via soil attached to the feet of animals. The seeds form a present to short-term persistent seed bank. *Myosurus minimus* is distributed throughout Europe, Western Asia and North America. The species can tolerate flooding, but usually is not able to respond morphologically or flower under flooded conditions. According to Brock and Casanova (1997) it can be regarded as an 'amphibious fluctuation tolerator'.

Peplis portula L., a species in the family Lythraceae (syn. *Lythrum portula* (L.) D.A. Webb), is a prostrate, creeping plant with opposite, spatula-shaped leaves. Under dry conditions the plant often has a reddish colour. When the plant grows submerged, the leaves are floating at the water surface. The small flowers appear in the leaf axils, with rose petals that can be missing. The flowering time ranges from July to September. One plant can produce between 14–557 capsules per plant with on average 27.2 seeds per capsule. The thousand-seed weight is on average 28 mg. The spherical seeds are released shortly after ripening and are dispersed via water or animals, forming a short-to long-term persistent seed bank. The species is distributed throughout Europe, North Africa and Asia. According to Brock and Casanova (1997) the species can be regarded as an 'amphibious fluctuation responder'.

Box 2 Habitus and seeds of the study species. Elatine alsinastrum 1 mm

From left to right: Plant emerging from the water surface; habitus after drawdown of the water level; seeds (red square = 1 mm)

Limosella aquatica From left to right: Habitus of the plant with stolons and flowers at the base of the rosette; seeds (red square = 1 mm)

Myosurus minimus From left to right: Habitus of the plant with elongated infructescences; fruits; seeds (red square = 1 mm)

Peplis portula From left to right: Habitus of the plant; seeds (red square = 1 mm)

Chapter 2

Effects of water regime and agricultural land use on diversity and species composition of vascular plants of temporary ponds in northeastern Germany¹

Abstract

Fluctuations of the water level at the edges of temporary water bodies provide favourable living conditions for annual plant communities of the phytosociological class Isoëto-Nanojuncetea. Such communities of periodically flooded ponds within the agricultural landscape of NE Germany are particularly rich in rare plant species of that class. During the past decades drainage, fertilisation and herbicides in the surrounding arable fields have led to a severe decline in diversity of these species. To develop efficient conservation strategies it is essential to understand the factors driving the species composition. Therefore, we studied how varying water regimes, soil properties and agricultural practices affect the diversity and species composition of these temporary ponds.

The study was carried out in seven ponds on a conventionally managed farm in NE Brandenburg. At each of these wetlands mixed soil samples were taken to determine the pH, total nitrogen and phosphorus concentration. The plant species were recorded in 177 plots, each covering 1 x 1 m². For each plot, the water level was recorded in April, July and August 2013, respectively, resulting in five 'water level regimes'. Total species number and percentages of Isoëto-Nanojuncetea species were determined per plot, to evaluate water level effects on the vegetation. In addition, mean Ellenberg

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indicator values for light, moisture and nutrients were calculated to assess the environmental conditions.

Kruskal-Wallis tests with subsequent multiple comparisons showed significant differences between water regimes in both total species richness and percentage of Isoëto-Nanojuncetea species. Isoëto-Nanojuncetea species established best at sites with fluctuating water levels. Fitting environmental variables to NMDS ordination axes indicated that the water regime was the most significant factor for floristic variation. In plots with a more uniform water regime the species composition was explained mainly by the soil fertility. Farming practices showed less pronounced effects on species composition.

Our results suggest that maintaining water regimes with fluctuating water levels and keeping nutrient content low are crucial for the successful conservation of Isoëto-Nanojuncetea communities in arable landscapes.

1. Introduction

Plants living at the shore of water bodies with dynamic water levels alternately have to cope with aquatic or terrestrial conditions. In Central Europe many species of these habitats belong to the class Isoëto-Nanojuncetea (Ellenberg and Leuschner, 2010). One of the main factors differentiating the species composition of this vegetation are species-specific germination requirements. Hejný (1957, 1962) divided the species of semi-terrestrial habitats into 'tenagophytes' (= plants of shallow waters) and 'pelochtophytes' (= plants of muddy littoral). Species of the first group are able to germinate in a completely flooded environment, whereas the latter preferably germinate in waterlogged soils. Additionally, the temperatures in water and soil affect the germination (Pietsch, 1999; Chytrý and Tichý, 2003; Kiesslich *et al.*, 2003). Small seed size, rapid germination, growth and reproduction under suitable conditions, and a long-term persistent seed bank are traits all species of semi-terrestrial habitats have in common (von Lampe, 1996; Thompson *et al.*, 1997; Poschlod *et al.*, 1999).

Natural habitats of these communities are riverbanks and the edges of shallow lakes. In the cultural landscape the species can also colonize pig pastures, drained fish ponds and wet parts of arable fields (Täuber, 2000). A common characteristic of these sites is the exclusion of competing plants by occasional flooding, tillage, trampling and uprooting animals.

During the past century this habitat type has experienced a severe decline due to the abandonment of traditional forms of land use and the reduction of flooding caused by more effective drainage (Kalettka, 1996; Deil, 2005). As a result, communities within the Isoëto-Nanojuncetea are threatened (Rennwald, 2000), and many characteristic species are considered rare and endangered (Ludwig and Schnittler, 1996).

To develop sustainable strategies to conserve this vegetation it is important to understand the individual habitat requirements of the respective species. To achieve a better understanding of the effects of water level dynamics on the species composition, we conducted a survey of seven ponds in an arable landscape of NE Germany. We address the following questions:

1. How does the flooding regime of the temporary ponds affect species composition and diversity?

2. Which flooding regime provides the most favourable conditions for species of the class Isoëto-Nanojuncetea?

3. How do farming and soil conditions influence the species composition?

4. Which management practices favour the establishment of rare and endangered Isoëto-Nanojuncetea species?

2. Materials and methods

Study area

The study was carried out in the year 2013 on two arable fields near Parstein, approx. 80 km northeast of Berlin, Germany (55 m a.s.l., N52°55', E14°02'). This area is known for its rich flora of Isoëto-Nanojuncetea species (Pietsch and Müller-Stoll, 1974). The area is part of the moraine landscape of the Pommern Stadium, which had been formed during the last glacial period (Weichsel). It is characterized by numerous kettle holes which are occasionally or permanently flooded. Most kettle holes in the study area presumably developed after the Medieval Age when extensive forest clearances induced soil erosion, which led to an accumulation of clayey impermeable layers in depressions and groundwater rise, because of reduced evapotranspiration after forest clearance (Klafs *et al.*, 1973). The water level of these so called 'pseudo-kettle holes' shows a particularly pronounced fluctuation. Here, glacial till formed fertile, alkaline Luvisols with almost neutral soil reaction.

The study area is characterized by a temperate, humid climate with a mean temperature of 8.3 °C and 532 mm precipitation (long-term mean from 1961–1990, weather station Angermünde; DWD, 2013b). The average temperature of the study year was 9 °C and had a precipitation of 483 mm (Angermünde; DWD, 2013a). Typical for the slightly continental climate are hot summers (long-term mean, 17 °C; 2013, 19 °C) with longer dry periods (long-term mean of summer precipitation, 177 mm; 2013, 165 mm; DWD, 2013c).

We investigated seven temporary ponds with an area of 0.2–1.6 ha, scattered over an area of 60 ha. To ensure comparability, all wetlands were situated within one farm that was conventionally managed.

Farming treatments

At the seven ponds, 177 sampling plots with 1 x 1 m² each were selected in summer 2012, based on to the occurrence of at least one of four characteristic species, i.e. *Elatine alsinastrum* L., *Limosella aquatica* L., *Myosurus minimus* L. and *Peplis portula* L. In autumn 2012, all plots were ploughed to ensure equal starting conditions, and excluded from agricultural management in the study year. To test the effects of different farming on species composition, combinations with and without crops, fertilization and herbicide applications, respectively, were randomly assigned to the plots and the corresponding treatment was applied manually. In addition, control plots

without any management were established. Winter wheat was sown in autumn 2012 (200 kg ha⁻¹), herbicides were applied in spring 2013 (Diflufenican, Flurtamone, Diflufenican), and fertilizer (in total 160 kg N ha⁻¹) in three consecutive applications.



Figure 3: Aerial picture of the study area with the seven wetlands (S1–S7) near Parstein in NE Brandenburg. The small map shows the location within Germany (orange dot). The blue shaded areas in the big map mark the highest flooding level of 2012 (digital orthophoto: Landesvermessung und Geobasisinformation Brandenburg, 2013).

Vegetation sampling and nomenclature

Plant species composition within the 177 plots was recorded at the beginning of August 2013. On each plot all vascular plant species were recorded. In addition, percentage cover of the herbal layer was estimated and the mean height of the vegetation measured. The nomenclature of plant species follows Wisskirchen and Haeupler (1998), for the phytosociological units Oberdorfer (2001); the assignment of

individual species to phytosociological classes follows (Ellenberg *et al.*, 2001). All vegetation samples and the environmental data are available in the Appendix (A2–A8).

Environmental variables

To characterise soil conditions, one representative mixed sample of the plough layer (0–20 cm) was taken from each of the seven wetlands in summer 2012. The samples were air dried and sieved with a 2 mm sieve. Measurements were conducted at the Adam Mickiewicz University Poznań, Poland. There, the pH (determined in 100 ml deionized water) and the concentrations of organic and ammonia nitrogen (digestion in sulphuric acid and colourimetrical determination of ammonia after absorption in boric acid), phosphorus (extraction in hot acidic aqueous solution and determination by molybdate method), and potassium (digestion in hydrochloric acid and determination using atomic emission spectrometry) in soil were analysed. The summary statistics of the soil properties are given in Table 1.

For each of the plots the mean Ellenberg indicator values for light (L), moisture (F) and nutrients (N) were calculated (Ellenberg *et al.*, 2001). Additionally, the number of species typical for the phytosociological class Isoëto-Nanojuncetea was determined per plot. Plant species were classified as belonging to the Isoëto-Nanojuncetea based on Ellenberg *et al.* (2001), when they are character species of any phytosociological group within the class (see Appendix, A2).

The water level of each plot was assessed three times in 2013, i.e. in mid-April, early July and early August, respectively. The observations were assigned to one of the categories 'moist', 'waterlogged' or 'flooded'. Plots were defined as moist, when the soil moisture was similar to the neighbouring arable fields. Waterlogged conditions were defined, when the soil was saturated but not covered by water. Plots with water level above the soil surface were defined as flooded. The observed combinations of water levels in April, July and August resulted in five 'water level regimes'.
Data analyses

The effects of water regime and farming practices on species richness were tested by carrying out Kruskal-Wallis tests with subsequent multiple comparisons of group means with Bonferroni correction to identify differences between the water level regimes. The tests were run using the package agricolae (de Mendiburu, 2014) within the software environment R (R Core Team, 2013).

		95 % conf.		
	median	interval mean	minimum	maximum
рН	6.8	±0.01	6.8	7.0
total nitrogen (mg kg ⁻¹)	1316	±176.89	1204	3920
total phosphorus (mg kg ⁻¹)	33.3	±0.49	31.8	39.3
potassium (mg kg ⁻¹)	78.5	±2.83	50.1	94.6

Table 1: Summary statistics of the measured chemical soil parameters of all seven wetlands.

In order to reveal patterns of floristic composition and their relationship to the different water regimes Nonmetric Multidimensional Scaling (NMDS) was used, where Bray-Curtis dissimilarities described distances between the samples (Faith *et al.*, 1987; Minchin, 1987). The ordination used three dimensions and was run with several random starts. Two plots (Ela38, Ela71) with only four and five species, respectively, were excluded from the ordination and model fitting.

To assess the environment-vegetation relationships linear trends and smooth surfaces of the environmental variables and the indicator values were fitted on the NMDS ordination. Generalized additive models were chosen to fit smooth surfaces with thin plate splines. The linearity of the relationship between environmental variables and the site scores was tested by comparing the coefficient of determination (R²) of a linear model fitting and a generalized additive model fitting (GAM). If the R² of the GAM was higher than that of the linear model, a non-linear relationship with the ordination result was assumed (Virtanen *et al.*, 2006). NMDS ordination and fitting of linear models was carried out using the R package vegan (Oksanen *et al.*, 2013).

3. Results

Overall vegetation patterns

In total, 70 plant species were recorded at the study ponds, including 54 broad-leaved herbs and 16 graminoids (see Appendix A2); 39 species were annuals and 31 perennials. According to phytosociological categories, six species belong to the class Isoëto-Nanojuncetea, among them the 'critically endangered' *Elatine alsinastrum* and *Juncus tenageia*, and the 'endangered' *Ranunculus sardous* (Ludwig and Schnittler, 1996). The most abundant species were *Tripleurospermum perforatum* (135 plots), *Polygonum aviculare* agg. (133), *Myosurus minimus* (116) and *Alopecurus aequalis* (100). Table 2 gives the mean frequencies of all species according to the five different water regimes.

Effects of water regime on species richness

The highest number of species was observed in plots with fluctuating water level ('moist-waterlogged-moist'; see Table 3); plots with a more constant water level had significantly fewer species ('flooded-flooded-moist', 'moist-moist-moist'; Kruskal-Wallis test, P < 0.001). The highest percentage of annuals was found in plots that were not flooded in spring ('waterlogged-flooded-moist', 'moist-moist-moist', 'moist-waterlogged-moist'), while the highest percentage of perennials was observed in spring-flooded plots ('flooded-flooded-moist', 'flooded-waterlogged-moist'). Furthermore, Isoëto-Nanojuncetea species dominated also in plots with fluctuating water levels and which were waterlogged at least during parts of the growing season ('flooded-flooded-moist', 'flooded-moist', 'waterlogged-flooded-moist', 'moist-waterlogged-moist'; Kruskal-Wallis test, P < 0.001, see Figure 4).

Effects of farming practices on species richness

The effects of farming were less clear than of the water regime. The highest species numbers were recorded in plots with crops and no other treatment, whereas lowest species numbers were observed under combined treatments of crop, fertilizer and herbicide application, and crop and herbicide application, respectively (Kruskal-Wallis test, P < 0.001, Figure 5A).

The proportion of Isoëto-Nanojuncetea species was highest in plots with only herbicide application. The lowest proportions were found in plots with fertilization as well as with combinations of crop and fertilization, crop and herbicide application, fertilization and herbicide treatment, respectively (Figure 5B).

Table 2: Mean constancy (%) of all species according to their appearance on plots with different water regimes. Each column represents all vegetation relevés of one water regime. Species are ordered according to their phytosociological status. Abbreviations of water regimes: For abbreviation of water levels see Figure 4. Last column gives the abbreviations of species names used in the NMDS plot.

	mmm	mwm	wfm	fwm	ffm	Abbreviations
number of relevés	120	6	31	5	13	of species
			-			names
Chenopodietea species						
Tripleurospermum perforatum	87	83	81			Tripperf
Chenopodium album	33	33				Chenalbu
Conyza canadensis	16					Conycana
Geranium dissectum	16					Geradiss
Persicaria maculosa	9	83	10			Persmacu
Stellaria media agg.	7					Stelmedi
Capsella bursa-pastoris	6					Capsburs
Chenopodium polyspermum	1		3			Chenpoly
Sonchus arvensis	1	17	•	•	•	Soncarve
Secalietea species						
Apera spica-venti	56					Aperspic
Fallopia convolvulus	46					Fallconv
Viola arvensis	37					Violarve
Anagallis arvensis	9	33	19			Anagarve

Vicia hirsuta	7					Vicihirs
Matricaria recutita	3					Matrrecu
Papaver rhoeas	3					Paparhoe
Artemisietea species						
Urtica dioica	8	33				Urtidioi
Stellaria aquatica	3			20		Stelagua
	mmm	mwm	wfm	fwm	ffm	Abbreviations
number of relevés	120	6	31	5	13	of species names
Artemisia vulgaris.	3					Artevulg
Molinio-Arrhenatheretea species						
Poa trivialis	10	17			•	Poatriv
Leontodon autumnalis	1					Leonautu
Myosotis scorpioides				80	62	Myosscor
Agrostietea species						
Myosurus minimus	72		87	60		Myosmini
Agrostis stolonifera	56	50	32		15	Agrostol
Plantago major ssp. intermedia	48	100	68	100	8	Planmajo
Trifolium hybridum	13					Trifhybr
Rumex crispus	12		48	80	46	Rumecris
Ranunculus sardous	7			•	•	Ranusard
Bidentetea species						
Alopecurus aequalis	52	83	48	100	100	Alopaequ
Rorippa palustris	30	83	55	60	38	Roripalu
Bidens frondosa	27		81		15	Bidefron
Rumex maritimus	23	17	26		23	Rumemari
Rumex palustris	4			40	69	Rumepalu
Persicaria lapathifolia	3		13			Perslapa
Persicaria minor	2	33				Persmino
Bidens cernua		83	10		15	Bidecern
Potentilla supina			19			Potesupi
Ranunculus sceleratus	•	17	•	20	•	Ranuscel
Isoëto-Nanojuncetea species						
Peplis portula	25	100	94	100	85	Peplport
Limosella aquatica	17		68	100	8	Limoaqua
Gnaphalium uliginosum	14	50	39			Gnapulig
Elatine alsinastrum	3	100	10	60	23	Elatalsi
Juncus bufonius	3	50	52			Juncbufo
Juncus tenageia			3	60	•	Junctena
-1 i i i						

Phragmitetea species

Phalaris arundinacea	8				8	Phalarun
Lycopus europaeus	4	83			8	Lycoeuro
Scutellaria galericulata	3				8	Scutgale
Oenanthe aquatica	3	50		80	92	Oenaaqua
Phragmites australis	1					Phraaust
Alisma lanceolatum		67	29	100	92	Alislanc
Epilobium parviflorum	3	33	39	20	8	Epilparv
	mmm	mwm	wfm	fwm	ffm	Abbreviations
number of relevés	120	6	31	5	13	of species names
Alisma plantago-aquatica			32	100	100	Alisplan
Bolboschoenus maritimus		•		20	•	Bolbmari
Eleocharis palustris		•		20	15	Eleopalu
Sparganium erectum		•		60	77	Sparerec
Typha latifolia	•	•		40	8	Typhlati
Other classes:						
Polygonum aviculare	87	83	61	40	15	Polyavic
Echinochloa crus-galli	55	100	87		•	Echicrus
Poa annua	49	17	94			Poaannu
Elymus repens	40		3			Elymrepe
Cirsium arvense	8		3	20		Cirsarve
Taraxacum officinale agg.	8	17				Taraoffi
Veronica arvensis	7					Veroarve
Lysimachia vulgaris	4					Lysivulg
Persicaria amphibia	4				46	Persamph
Medicago lupulina	2					Medilupu
Juncus articulatus	2	17				Juncarti
Tussilago farfara	1					Tussfarf
Vicia sepium	1					Vicisepi
Trifolium campestre			10			Trifcamp

Table 3: Annual, perennial and total species numbers(mean ± SD) and numbers and percentage ofIsoëto-Nanojuncetea species (I-N) under different water regimes. For abbreviation of water levels seeFigure 4.

Wate	er regime	Annual	Perennial	Total	I-N species	I-N species (%)
mmm	(n = 122)	7.5 ± 2.3	2.9 ± 1.3	10.4 ± 2.9	1.1 ± 1.3	9.8 ± 10.8
mwm	(n = 6)	10.2 ± 1.3	5.2 ± 1.8	15.3 ± 1.9	4.0 ± 1.1	25.8 ± 5.0
wfm	(n = 31)	9.2 ± 2.0	3.0 ± 1.5	12.2 ± 2.5	3.5 ± 1.1	29.1 ± 8.3

fwm	(n = 5)	6.2 ± 1.5	7.6 ± 1.3	13.8 ± 2.6	4.2 ± 0.8	30.5 ± 3.3
ffm	(n = 13)	3.9 ± 1.5	6.0 ± 1.2	9.9 ± 2.0	1.2 ± 0.8	12.3 ± 7.5



Figure 4: Boxplots of number of species (A) and percentage of Isoëto-Nanojuncetea species (B) under different water regimes (multiple comparisons, $\alpha = 0.05$).

Lowercase letters indicate differences between groups. Abbreviations of water levels in April-July-August: mmm, moist-moist-moist; mwm, moist-waterlogged-moist; wfm, waterlogged-floodedmoist; fwm, flooded-waterlogged-moist; and ffm, flooded-flooded-moist.



Figure 5: Effects of farming practices on the total number of species (A) and on the percentage of Isoëto-Nanojuncetea species (B).

Lowercase letters indicate differences between groups. Abbreviations of treatments: c, crop; cf, crop and fertilizer; cfh, crop, fertilizer and herbicide; ch, crop and herbicide; f, fertilizer; fh, fertilizer and herbicide; h, herbicide; and o, control without treatment.

Effects on species composition

Nonmetric Multidimensional Scaling (NMDS) mainly ordered the sampling plots along a moisture gradient (Figure 6). Species belonging to arable plant communities (Secalietea cerealis, Chenopodietea; Figure 7) represented the largest group and were mostly located on the left hand side of the ordination, representing drier sites, which were never flooded, and therefore allowed the development of typical arable plant communities. Most of them were common weeds which indicate regularly managed arable fields (*Apera spica-venti, Chenopodium album* agg., *Echinochloa crus-galli, Tripleurospermum perforatum*). The species plotted in the upper right and in the centre of the ordination represented a mixture of plants belonging to frequently disturbed (Isoëto-Nanojuncetea, Bidentetea tripartitae) and unfrequently disturbed communities of temporary ponds (Agrostietea stoloniferae). Species adapted to permanent flooding (Phragmiti-Magnocaricetea), like *Alisma plantago-aquatica* and *Sparganium erectum*, were displayed at the lower right.



Figure 6: NMDS ordination plot of all sampling plots (stress 15.3%). Different water regimes are marked by different colours. To improve readability species names are not shown.



Figure 7: NMDS plot of all species (stress 15.3%). Species belonging to one phytosociological class are marked by the same colour. Species were assigned to phytosociological units according to (Ellenberg *et al.*, 2001). Species which couldn't be assigned to one certain phytosociological class or phytosociological classes which contained only one or two species were marked black. To improve readability species names are abbreviated and sites are not shown. In Table 2 all species names are listed with their corresponding abbreviations.

Figure 8 shows an overlay of the NMDS ordination with the fitted vectors and smoothed surfaces for the mean Ellenberg indicator values and plant height. The strongest linear correlation to the ordination space ($R^2 = 0.90$) was found for soil moisture values. The values in Figure 8A represented a gradient from moderate soil moisture at the left (mean 5.5) to values of 9 indicating wet sites at the right side of the plot. As the mean Ellenberg indicator value for light was highly correlated with the mean indicator value for moisture ($R^2 = 0.68$, P < 0.001), it was also closely related to the first NMDS dimension (Figure 8B). The mean vegetation height described an orthogonal gradient with low growing communities in the upper part of the plot and taller plants at the opposite side (Figure 8C). Collinearity between the fitted surface for the mean vegetation height and the nitrogen indicator values (Figure 8D) suggested a soil fertility gradient along the second NMDS dimension. Measured soil factors revealed little variation among the seven ponds, except for nitrogen, which showed one outlier (Table 1); due to this low variation and few samples we did not plot these values on the NMDS ordination. The different farming practices had only a low correlation to the site scores ($R^2 = 0.11$, P < 0.01), indicating that farming only had a minor impact on sites with water level fluctuations (Table 4).



Figure 8: NMDS ordination with fitted vectors and smoothed surfaces for the mean Ellenberg indicator values for A: soil moisture (F), B: light (L), C: the mean vegetation height (hmean) and D: nutrients (N). The coefficient of determination (R²) is given for the linear and the surface fit. Arrows indicate the direction of the most rapid change along the gradient. Sampling plots are marked by grey circles, species names are not shown.

Table 4: Results of the vector and smoothed surfaces fitting of the environmental variables. Values given in the columns NMDS1 and NMDS2 represent the direction cosines of continuous variables along the two axes. P values are based on 999 random permutations. Code for significance levels: *, P < 0.05; **, P < 0.01; ***, P < 0.001; N.S., P > 0.05.

	Linear Model Fit						Surface	
	NMDS1	NMDS2	R²	Р		R ²	Р	
Mean height	-0.13	-0.99	0.41	0.001	***	0.48	0.001	***
рН	-0.87	0.20	0.37	0.001	***	0.52	0.001	***
Phosphorus	-0.18	0.84	0.49	0.001	***	0.49	0.001	***
Potassium	0.07	-0.99	0.04	0.066		0.26	0.001	***
Nitrogen	0.05	0.44	0.38	0.001	***	0.08	0.001	***
L	0.63	-0.31	0.62	0.001	***	0.48	0.001	***
F	0.96	-0.28	0.90	0.001	***	0.90	0.001	***
Ν	-0.56	-0.83	0.11	0.001	***	0.18	0.001	***
Factors:								
Treatment			0.11	0.002	**			
Water regime			0.47	0.001	***			

4. Discussion

Richness of Isoëto-Nanojuncetea species

Dreger (2002) found within the biosphere reserve Schorfheide-Chorin similar species numbers for small kettle holes (<1 ha). Fischer (1983) and Hoffmann *et al.* (2000) reported similar numbers of endangered species in other parts of Brandenburg. The number of Isoëto-Nanojuncetea species within our study was reasonably low. This can be related to the unfavourable weather conditions during the study year, as Pietsch and Müller-Stoll (1974) noted, that several factors like the weather conditions and the management of the fields influence the opportunity to find species of the dwarf rush communities.

Effects of water regime and farming on species richness

Our investigations showed that strong fluctuations of the water level with flooding in spring or summer positively affect both the total richness of vascular plants and the number of Isoëto-Nanojuncetea species. We suppose that these site conditions favour high species numbers by increasing the range of favourable habitat conditions. These results are consistent with Greet *et al.* (2013) that duration and frequency of flooding positively affect the plant species richness in amphibious habitats including the Isoëto-Nanojuncetea and related communities. A study on Australian temporary wetlands contrastingly resulted in highest total species richness without any inundation (Casanova and Brock, 2000). These contradicting results may be due to differences in the study sites. The Australian study was conducted at wetlands surrounded by relatively undisturbed grass- und shrublands, whereas in our study regular farming may have reduced the diversity of the arable plant community, which would dominate these sites under terrestrial conditions.

An unexpected result concerning the arable farming treatments was that richness of Isoëto-Nanojuncetea species was highest in plots solely treated with herbicides. As most Isoëto-Nanojuncetea species germinate well after application of pre-emergence herbicides, they may be scarcely affected by this treatment and possibly benefit from the reduced competition of other species (Poschlod *et al.*, 1999). This also matches with Brose and Tielbörger (2005) who found that removal of competitive species can increase the richness of wetland species. However, as our study covers the time span of only one year (with unfavourable germination conditions) and we tested only one herbicide, more detailed investigations are necessary before general conclusions on the effects of herbicides on Isoëto-Nanojuncetea species are possible. Fertilization and competition by crops resulted in particularly low numbers of such species.

Effects of water regime on community composition

Ordination of plant communities of the 177 plots with differing water regimes, soil properties and farming practices revealed fluctuations of the water level to be most decisive for community composition. Casanova and Brock (2000) and Brock *et al.* (2005) came to the same conclusions by testing effects of different water regimes on the establishment of wetland plant communities in seed bank investigations. A long-term study on the effects of the timing of flooding on the species composition showed that seasonality (flooding in spring or summer) altered the community more than the frequency of flooding (Robertson *et al.*, 2001). Also other studies showed that flooding in general, and duration of flooding in particular, control the composition of wetland communities (Brock *et al.*, 2005; Cherry and Gough, 2006; Robertson and James, 2007; Della Bella *et al.*, 2008). Pätzig *et al.* (2012) found annual 'hydro-period' (defined as the number of months a site was flooded) to be significantly related to the occurrence of amphibious plants.

Mean Ellenberg indicator values for moisture and light showed a strong relationship with the first ordination axis, representing the influence of the water level fluctuations on the plant species composition. This result agrees with Täuber and Petersen (2000) who found that the water regime and availability of light both are essential factor for the successful establishment of Isoëto-Nanojuncetea species. Germination experiments by Salisbury (1970) and Poschlod *et al.* (1999) demonstrated that an insufficient light supply can limit germination of these species in deep water bodies. Mean vegetation height and the mean Ellenberg indicator value for nutrients showed a good relationship to the floristic variation, indicating that the communities emerging under different water regimes are related to the nutrient content in the soil. Similar conclusions were drawn by Pätzig *et al.* (2012) who found a positive relationship of nitrate-nitrogen in the water to amphibious plants. Depending on the soil nutrient content, Isoëto-Nanojuncetea communities establish under low or medium nutrient levels and they are replaced by more nitrophilous Bidentetea communities (Kiesslich *et al.*, 2003).

Implications for conservation and management

As temporary ponds are well known for their richness of annual species and often harbour numerous rare and endangered species, they significantly contribute to the biodiversity of the study area in NE Brandenburg (Dreger, 2002) and similar agricultural landscapes (Davies *et al.*, 2008). The main factors creating suitable habitat conditions for the Isoëto-Nanojuncetea as well as other plant communities, like those within the class Bidentetea, in arable fields are regular human disturbances by ploughing and the change between flooding and drought. Drainage or local excavation of temporary ponds, as it took place during the past century (Kalettka, 1996) and is still done by some farmers, severely threaten these plant communities by discontinuing the water level fluctuations. Even macrophyte communities, which also harbour several rare and endangered plant species (Raabe, 2008; Pukacz *et al.*, 2009) and offer breeding habitat for some amphibian species, benefit from the regular ploughing and the water level fluctuations. Observations during the past 8 years confirm that the species richness and the number of rare plant species are remarkably higher in temporary ponds than in perennial ponds in the study area (U. Raabe, unpubl. results).

Furthermore, also setting aside these areas as suggested by Berger *et al.* (2003) would cause a decline of the Isoëto-Nanojuncetea communities in favour of mid- and late-successional plant communities which are of less conservation concern. As all these communities contribute to the species richness of these field ponds, a more

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differentiated management is recommended that would creating or saving a high diversity of habitat types at temporary ponds.

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Supplements and Appendices

Supplementary information can be found in the Appendix

Appendix A2. Species traits, classification as Isoëto-Nanojuncetea species and assignment to phytosociological classes.

Appendix A3. Site parameters of all plots of temporary wetlands in Brandenburg.

Appendix A4. Vegetation relevés of all plots with water levels dry-dry-dry in April-July-August.

Appendix A5. Vegetation relevés of all plots with water levels dry-waterlogged-dry in April-July-August.

Appendix A6. Vegetation relevés of all plots with water levels flooded-waterlogged-dry in April-July-August.

Appendix A7. Vegetation relevés of all plots with water levels waterlogged-flooded-dry in April-July-August.

Appendix A8. Vegetation relevés of all plots with water levels flooded-flooded-dry in April-July-August.

Chapter 3

Managing plant species diversity under fluctuating wetland conditions – the case of temporarily flooded depressions²

Abstract

Temporarily flooded depressions in arable fields support populations of specialized plant species that are affected both by flooding and agricultural management. Depending on the degree of flooding different proportions of wetland and arable species contribute to the seed bank. This is reflected by high inter-annual variation in plant communities with high conservation value. Due to on-going agricultural intensification, biodiversity of temporarily flooded depressions has declined, and several plant species have become regionally extinct. Seed banks can harbour persistent seeds over long periods of time, and can play a crucial role for conservation and restoration of temporary wetland vegetation.

This study focuses on effects of different flooding regimes on plant species emerging from seed banks of temporarily flooded depressions in arable fields in NE Germany. We cultivated soil samples from upper and lower wetland zones under short, intermediate and long-term flooding (5, 15 and 40 cm above soil surface) in a common garden experiment for 2 years. We observed significant changes in species composition depending on flooding duration. Species richness declined, whereas evenness increased with increasing flooding duration. Upper and lower zones showed similar species richness and evenness, but differed in species composition. Red List species emerged from all treatments while species identity differed, indicating that all

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communities emerging under different flooding regimes have high conservation value. The study indicates that seed banks under fluctuating site conditions can constitute a series of alternating plant communities. This could be used to develop management strategies which benefit different communities with high conservation values.

1. Introduction

Seed banks have a great potential for conservation and restoration of degraded habitats since they may contain seeds of regionally extinct species (Poschlod, 1993; Bernhardt et al., 2004). Especially, in ecosystems with environmental fluctuations many species only emerge periodically and survive unfavourable periods in the seed bank (Poschlod et al., 1999). The dynamics of such systems favour contrasting plant communities depending on the site conditions, and the seed bank will reflect these different communities. Adaptive management may facilitate the establishment of a series of alternating communities, thus, maximising plant diversity over time. Many conservation studies have dealt with assessing the soil seed bank and its importance for the conservation and restoration of wetlands in agricultural landscapes (Bissels et al., 2005; Casanova, 2012). In the prairie pothole region and in coastal plain depressions in the U.S.A., for example, several studies have focused on studying different approaches to restore the natural vegetation after long-term agricultural use of these wetlands (Galatowitsch and van der Valk, 1996; De Steven et al., 2006). Other studies focused on restoring wet meadows after long periods of intensive (arable) land use, using the soil seed bank (Bekker et al., 2000; Hölzel and Otte, 2004; van Dijk et al., 2007). However, studies assessing the soil seed bank of temporarily flooded depressions in arable fields within temperate climates have been rare, so far (Bissels et al., 2005).

Due to intensification of agricultural management, many regions which formerly harboured a great variety of species specifically adapted to traditional farming practices have experienced considerable losses in arable plant diversity in the past decades (Burrichter *et al.*, 1993; Meyer *et al.*, 2013; van Zanten *et al.*, 2014). One example are wet field depressions that have been ameliorated by more efficient drainage. Many arable, as well as amphibious plant species are adapted to disturbance

and variable site conditions by developing a long-term persistent seed bank (Thompson *et al.*, 1998; Brock, 2011). In temporarily flooded fields both regular arable weeds and wetland plants are found in the seed bank (Albrecht, 1999; Bissels *et al.*, 2005). Thus, the soil seed bank of such sites can harbour complementary plant communities that markedly exceed the species diversity in the apparent vegetation.

In large parts of Europe, deforestation during the Medieval Age promoted the development of wet field depressions due to rising ground water levels that in turn, led to the flooding of local depressions, where colluvial deposits of clay inhibited the infiltration of water (Klafs *et al.*, 1973). Such man-made wetlands also developed in abandoned marl or clay pits (Day *et al.*, 1982). As habitat quality has deteriorated due to widespread drainage, biodiversity of these habitats has steeply declined with many plant species being threatened by the loss of flooding and water level fluctuations (Zacharias and Zamparas, 2010). Moreover, climate change is expected to have a negative impact on temporarily flooded depressions, as the weather is predicted to become more extreme with mild wet winters, and hot dry summers (IPCC, 2007). This may shorten flooding duration and thus disadvantage plant species that require flooding for germination (e.g. Kwon *et al.*, 2013). On the other hand, precipitation is predicted to become more uneven and more intense (Madsen *et al.*, 2009), which could benefit species assemblages from temporarily flooded depressions (Kappelle *et al.*, 1999). Thus, new concepts are needed to preserve the vegetation of these habitats.

The actual vegetation developing in temporarily flooded depressions in arable fields depends on agricultural management, soil and climatic conditions (Pinke *et al.*, 2014). Most important, species diversity of these depressions is affected by the flooding regime (Casanova and Brock, 2000), controlling germination via soil temperature, light and oxygen concentration (e.g. Matsuo *et al.*, 1984). At the initial stage of secondary succession, competition is low and most species best establish under terrestrial conditions as long as soil moisture is sufficient. Only submersed macrophytes and those with floating leaves are unable to survive at terrestrial sites, and most of them do not establish without inundation (Baskin and Baskin, 2014). During flooding the depth of waterbodies can affect germination of water plants through daily changes in light

availability and temperature (Pons and Schröder, 1986). High water levels and a long duration of flooding promote water plant species, whereas a short flooding duration is more advantageous for terrestrial species. During the drawdown amphibious plant species can emerge and under damp but not flooded conditions also terrestrial species can emerge. Intermediate flooding duration, with a slow drawdown or slowly rising water levels throughout a vegetation period, can stimulate a sequence of species, water plant species, amphibious plants or terrestrial species. Thus, highest species diversity is expected for intermediate flooding. Moreover, as temporary wetlands harbour many rare and endangered plant species (Casanova and Brock, 1990; Lentz and Dunson, 1999; Mann and Raju, 2002; Pukacz et al., 2009; Lukacs et al., 2013), the number of Red list species will increase with flooding. The species evenness often is negatively correlated to the species richness (Weiher and Keddy, 1999). In aquatic ecosystems limited availability of light and chemical growth factors can significantly limit competition by reduced productivity of dominant species (Slivitzky, 2002; Li et al., 2015). On the other hand, this may also reduce species richness by excluding species without appropriate adaptation However, as dominance is reduced and most of the remaining species find suitable conditions to establish we expect that species are more likely to be equally abundant and that evenness will increase with intensity of flooding. In the lower wetland zone that experiences flooding more frequently and where flooding duration is more likely to be longer than in the upper wetland zone, seeds can accumulate in the soil, since germination of most species is inhibited under anaerobic conditions (Saatkamp et al., 2014). Moreover, as flooding gradients lead to differences in species composition in the apparent vegetation (Keddy and Reznicek, 1986), a similar pattern can be expected for the composition of the soil seed bank. Thus, we expect the soil seed bank to reflect the flooding history of the different wetland zones.

In this study we investigate how soil seed banks in the upper and lower wetland zone of temporarily flooded depressions reflect the past flooding regime, and how flood management could be used to create a series of different plant communities. We analyse species diversity of plant communities emerging from soil samples in

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experiments with differing flooding duration and water levels. Specifically, we hypothesize that:

- Plant communities emerging from the seed bank are different along a flooding gradient, both in the upper and lower zone of temporarily flooded depressions.
- Seedling densities emerging from the seed bank are highest at intermediate flooding, especially in samples from the lower zone.
- (iii) Species richness of the seed bank decrease with flooding in samples from the upper zone.
- (iv) Species evenness is highest at high flooding in both zones.
- (v) The number of rare species increases with flooding.

2. Methods

Study sites and seed bank sampling

Soil samples were collected at Parstein, NE Germany (northeast of Berlin, 53°0'52 N, 13°59' E, 55 m a.s.l.). This region is characterized by a temperate, humid climate with an average annual temperature of 9 °C and 500 mm precipitation (1981–2010; DWD, 2014), one third of the precipitation occurring in summer. The glacial moraine landscape has fertile luvisols with an almost neutral soil reaction. Glacial processes and former land use resulted in numerous wet field depressions with great differences in both frequency and duration of flooding (Klafs *et al.*, 1973). As natural and man-made depressions have many ecological characteristics in common we refer to both of them as 'temporarily flooded depressions'.

All samples were taken from seven temporarily flooded field depressions within an area of 60 ha. They were selected on the presence of *Elatine alsinastrum*, a rare and endangered amphibious species (Ludwig and Schnittler, 1996; Landesumweltamt, 2006; Lansdown, 2014). Due to restricted distribution of this species and to facilitate field access and soil collection, samples were taken on one conventionally managed farm. According to information from the farmer, the arable fields were cultivated in a

four-course crop rotation (winter barley, winter rape, winter wheat, maize) using field cultivator and disc harrow (plough level 0.2 m) for soil tillage and applying mineral NPK fertilisers and herbicides depending on nutrient needs of crops and weed abundance. All temporarily flooded parts were cultivated if the water level and soil moisture content allowed the use of machinery. In May 2012, the size of the waterbodies was 0.3–4.2 ha, with geographical distances between 0.2–1.0 km (mean 0.5 km; see Figure 9).



Figure 9: Position of the seven temporarily flooded depressions (shaded areas) within two arable fields. Aerial picture from Bing (2012).

As the vegetation at the edges of wetlands follows a clear zonation according to soil moisture and flooding (Keddy and Ellis, 1985), we assumed that such a zonation might also exist in the seed bank composition. Therefore, we differentiated between the upper zone that was flooded until late May, and the lower zone that was flooded until late July.

In August 2012, we took soil samples from both of these zones. At depressions with permanently flooded core areas (marked by a shoreline with perennial plants like *Salix* spp. or *Phragmites australis*); permanently flooded parts experience a different disturbance regime than arable fields. Therefore, we also presumed differences in the species composition of the soil seed bank and excluded these parts from sampling. At each depression, 30 soil cores were randomly collected from both the upper and lower zone. Soil corers had diameters of 3.3 cm, and samples were taken down to -20 cm corresponding to the depth of ploughing practiced on the farm. According to Gruber *et al.* (2010) regular tillage leads to an even seed distribution within this plough layer. The samples of each zone were put together mixed thoroughly to remove site-specific seed bank variation. This resulted in two composite samples, from the upper and lower zone, respectively, representing contrasting flooding history.

Flooding experiment

To test the effects of different combinations of water level and flooding duration on the emergence of plant communities, the composite samples were transferred to a set of artificial outdoor water basins and split up into different treatments. As the depressions in the study area were usually flooded in winter also the samples in the basins were kept flooded at that time. We defined the start of the vegetation period as the first week with mean daily temperatures above 5 °C, which was early April in 2013 and early March in 2014. Usually, the upper zone of flooded field depressions dried up within about 2 weeks after the start of the vegetation period, in the lower zone this took approximately 8 weeks (S. Altenfelder, pers. obs.). Therefore, we chose flooding durations of 2 and 8 weeks. To examine the full gradient of possible flooding durations, we included a permanently flooded treatment (>16 weeks flooded) and an unflooded control (water level 15 cm below soil surface). To test for the effects of different water levels, we established water levels of 5, 15 and 40 cm above the soil surface. Moreover, each water level was combined with three flooding treatments (2, 8, >16 weeks). All combinations of flooding duration and water level resulted in 10 treatments that can be interpreted as gradients of flooding intensity.

For each treatment combination we used six replicates, resulting in a total of 118 plastic pots (18 x 18 x 18 cm³). Approximately three quarters of each pot were filled with sterilised soil and covered with 2 cm soil from the upper or lower zone. To evaluate any seed contamination, we additionally set up controls with autoclaved soil (four replicates per flooding treatment and six replicates for the unflooded control). Since *Epilobium* spp., *Juncus effucus, Lythrum salicaria, Sonchus arvensis* and *Taraxacum* spp. emerged from these pots we considered them as seed contaminants and excluded them from further analyses. Nomenclature follows Wisskirchen and Haeupler (1998) for vascular plants, and Blümel and Raabe (2004) for charophytes.

The experiment started in August 2012 and ran for 2 years until August 2014. All emerging seedlings were identified, counted and removed in bi-weekly sampling over the whole study period and soil was mixed when seedling emergence declined. Plants which were difficult to identify were grown until they could be assigned to a certain species. Within the *Alisma plantago-aquatica* group three different taxa occurred, however, as most individuals did not flower, it was impossible to determine their abundance. The Red List of the Federal State of Brandenburg (Landesumweltamt, 2006; Kabus and Mauersberger, 2011) was used to assess the conservation value of plants emerging from the soil samples.

Data analyses

Seed numbers were calculated by extrapolating the numbers of seeds detected in the surface area of the soil cores to one m². Two pots of the upper zone (2 weeks at 40 cm; permanently flooded 40 cm) were lost during the experiment and thus had to be removed from the analyses.

Response variables were species richness, evenness of seedling communities, and number of Red List species as a measure for the conservation value. These variables could not be transformed to achieve a normal distribution. Therefore, we performed Kruskal-Wallis tests using the package agricolae (de Mendiburu, 2014) in the statistic environment R (R Core Team, 2013) to determine the effects of water level and flooding duration on soil samples. As the two wetland zones did not significantly differ in seedling density, species richness, evenness, and conservation value (Figure 10) these zones were no longer distinguished in further analyses. To test for differences between the different treatment combinations, group means were compared at the 95% confidence interval with Bonferroni corrections. Interaction effects were tested using dummy variables. As a measure for evenness we calculated Pielou's J (J = H'/ln s), with $H' = -\Sigma p_i x \ln p_i$, where p_i is the proportional abundance of species *i*, and *s* is the number of species. For calculation of the number of Red List species we included species with a Red List status 'near-threatened', 'vulnerable', 'endangered' and 'critically endangered'.



Figure 10: Species richness (a), seedling density (b), evenness (c) and number of Red List species (d) in the soil seed bank of the upper ('aquatic') and lower ('terrestrial') zone of temporarily flooded depressions in arable fields (Kruskal-Wallis test, P < 0.05).

In order to identify major gradients in species composition, a detrended correspondence analysis (DCA) was used (Hill and Gauch, 1980). We preferred this method to non-metric multidimensional scaling (NMDS) since both operations led to almost identical results (results of NMDS not shown) and, as detrending fits species response curves to standard deviations, DCA provides more detailed information on beta diversity along the first ordination axis. The effect of high seedling densities was reduced by square root transformation and subsequent Wisconsin double standardization. To assess relationships between seedling composition and different water regimes linear trends of water level, flooding duration and median Ellenberg indicator values for moisture (Ellenberg *et al.*, 2001) were fitted on the ordination results. Both ordination and fitting of linear models were carried out using the R package vegan (Oksanen *et al.*, 2013).

3. Results

Effects on diversity

During the two years sampling period, a total of 19966 seedlings emerged from all samples. Seedling density was highest under no flooding (74282 ± 15015 seedlings m⁻², mean ± SD) or short-term flooding (71427 ± 15015 seedlings m⁻²). It decreased with increasing duration of inundation (Kruskal-Wallis test: H = 105.0, P < 0.0001; Figure 11). Under intermediate and long-term flooding there was an effect of water level, with higher seedling densities at water tables of 5 cm compared to higher water levels within the same flooding duration treatment.

A total of 65 species emerged from the soil samples, nine of them being considered as endangered according to the Red List of the Federal State of Brandenburg (see Appendix A9). In total, 54 species emerged from soil samples from the upper zone and 60 from the lower zone, with 49 species in common. The most abundant species were *Alisma plantago-aquatica* agg. and *Peplis portula*, which both emerged from 93 % of all pots.



Figure 11: Differences in seedling emergence from soil samples of temporarily flooded depressions in arable fields in response to experimental flooding.

Lowercase letters indicate significant differences among groups according to multiple comparisons following Kruskal-Wallis test (P < 0.05).



Figure 12: Species richness in soil samples from temporarily flooded depressions in arable fields under experimental flooding.

Lowercase letters indicate significant differences among groups according to multiple comparisons following Kruskal-Wallis test (P < 0.05).

Species richness was highest under no and short-term flooding (22 ± 2 species per pot with no flooding and 22 ± 3 with short-term flooding). Flooding duration significantly reduced species richness (Kruskal-Wallis test: H = 88.1, P < 0.0001); water level had no effect on species richness (Figure 12). Evenness significantly increased with increasing flooding duration (Kruskal-Wallis test: H = 86.7, P < 0.0001; Figure 13), while water level had no effect on the evenness.





Lowercase letters indicate significant differences according to multiple comparisons following Kruskal-Wallis test (P < 0.05).



Figure 14: Red list species emerging from soil samples of temporarily flooded depressions in arable fields under experimental flooding.

Lower case letters indicate significant differences according to multiple comparisons following Kruskal-Wallis test (P < 0.05).

Highest numbers of Red List species were observed under no or short-term, as well as intermediate flooding with shallow water levels (no flooding: 5.1 ± 0.5 ; short term flooding: 5.1 ± 0.6 ; intermediate with water level 5 cm: 5.2 ± 0.6 Red List species per sample). Increasing flooding duration decreased number of Red List species significantly (Kruskal-Wallis test: H = 67.9, P < 0.0001; Figure 14). Water level changed Red List species numbers under intermediate and long-term flooding between 5 cm and 40 cm water levels. In the unflooded and temporarily flooded treatments almost all emerging Red List species were amphibious plants, including *Elatine alsinastrum*, *Limosella aquatica* and *Myosurus minimus*. Under permanent flooding these species also emerged but more rarely; instead, the threatened charophyte *Tolypella prolifera* exclusively emerged under intermediate or permanent flooding.

Variation in species composition along a flooding gradient

The value of 3.7 for length of gradient along the first ordination axis of DCA indicated an almost complete turnover in plant species composition emerging from soil samples (Figure 15). This gradient was mainly determined by differences between temporary and permanent flooding; few differences were observed among the unflooded and short- to intermediate-term flooded treatments. The gradient was closely correlated with flooding duration and indicator values for moisture (P < 0.001, Table 5). Along the second ordination axis the species composition changed according to the wetland zone (P < 0.001, Table 5). This gradient indicates that species composition among both wetland zones increasingly differed with flooding duration. The experimental water levels were not significantly correlated with the species composition.



Figure 15: Detrended Correspondence Analysis (DCA) of species composition in soil samples responding to experimental flooding from the upper (filled symbols) and lower zone (transparent symbols) of temporarily flooded depressions in arable fields.

Arrows indicate the correlation of flooding duration and the median Ellenberg indicator values for moisture (EIV moisture) to the ordination results from linear models. Length of the arrows indicates the strength of the correlation. Different flooding durations are represented by different symbols; species without Red List status are represented by '+'. Full names of Red List species: *Butomus umbellatus, Elatine alsinastrum, Galium palustre* agg., *Juncus tenageia, Limosella aquatica, Myosurus minimus, Peplis portula, Potentilla supina* and *Tolypella prolifera*.

Table 5: Relationship between flooding duration, median Ellenberg indicator value for soil moisture (EIV moisture), water level and wetland zone and the first two DCA axes. P-values are based on 999 random permutations. Bold P-values indicate significant correlations.

	DCA Axis 1	DCA Axis 2	R²	P-value
Flooding duration	0.994	-0.107	0.8	0.001
EIV moisture	0.850	-0.527	0.7	0.001
Water level	0.683	0.730	0.0	0.080
Upper wetland zone	0.034	0.301		
Lower wetland zone	-0.032	-0.291		
Wetland zone			0.1	0.001

4. Discussion

Effects on seedling abundances, diversity and conservation value

Contrary to our hypotheses, the seedling abundance as well as species richness were highest with no or short-term experimental flooding. It made no difference whether samples came from the upper or lower wetland zone. This agrees with other studies, where highest species richness was observed in unflooded samples (Casanova and Brock, 2000; Aponte et al., 2010). The cause for these high numbers of seedlings and species establishing from the soil seed bank is that both terrestrial and amphibious plant species find suitable germination conditions when flooding is short or absent, as long as competition is low. Furthermore, many amphibious plant species emerge in high numbers, as soon as environmental conditions favour germination (von Lampe, 1996; Bliss and Zedler, 1998). Under flooded conditions, where temperatures are constant during day and night, most amphibious plants fail to germinate, as they need diurnally fluctuating temperatures (Poschlod et al., 1999; Baskin and Baskin, 2014). Furthermore, only few species are known to germinate better when they are submerged (Poschlod et al., 1999), and seedling densities are usually higher under unflooded conditions (Collins et al., 2013). Obligate water plants, such as Tolypella prolifera, which depend on continuous flooding, emerged only to a minor extent in all

treatments and therefore they did not significantly contribute to the species richness in the temporary flooded treatments.

In our study evenness increased with flooding duration. This observation is consistent with findings of Weiher and Keddy (1999) in riverine wetlands, where species evenness also increased with decreasing species richness and abundance. These results may be caused by increasing stress which is strengthened with flooding duration. Thus, species unable to tolerate flooding are inhibited and species richness decreases. The remaining stress-tolerant species are more likely to emerge with similar abundances leading to an increased evenness. As stress is usually associated with decreasing plant biomass and size (Grime, 1979), decreased importance of competitive interactions could favour small-sized species contributing to plant communities with low species richness but high evenness where all species present were equally uncommon (Bock et al., 2007). On the other hand, there also are studies that found inconsistent patterns for species richness and evenness (Stirling and Wilsey, 2001; Soininen et al., 2012). They conclude that both measures of biodiversity depend on different and independent ecological processes. Thus, Ma (2005) related these patterns to a deviating response to soil conditions, i.e. C:N ratio and phosphorus concentration. In our study, however, such effects can be excluded since we thoroughly mixed the soil samples.

We used the number of Red List species as an indicator for the conservation value of the plant communities emerging from the soil samples. From other studies it is known that this conservation value of temporarily flooded depressions can be very high (Casanova and Brock, 1990; Bell *et al.*, 2012; Lukacs *et al.*, 2013). Indeed, we also found endangered species in most soil samples. This indicates that the soil seed banks of temporary wetlands are an important reservoir for rare species, which can be activated for conservation purposes or used during restoration of degraded sites. Faist *et al.* (2013) reported species being rare in the aboveground vegetation to be more abundant in the seed bank in vernal pools in California, showing the potential for future establishment of rare species from the seed bank.

As in other studies on the soil seed bank of wetlands (e.g. Aponte *et al.*, 2010), a few species account for the main share of the seed bank , which is a common characteristic

for this habitat type (Harper, 1987). Some rare plants that are reported for the study area, such as *Schoenoplectus supinus* and *Chara baueri*, could not be found (Hoffmann, 1996; Raabe, 2009). This might be due to their rarity and the limited amount of soil analysed. The differences in the number of Red List species between the different experimental flooding regimes were marginal, but all species groups from terrestrial to amphibious and water plants were included. This result indicates favourable conditions to promote endangered species from different plant communities along a flooding gradient.

There were no differences in seedling abundance, diversity or conservation value between the upper and lower wetland zone. This shows that even in the areas that are less frequently flooded and farmed when dry enough, the diversity and conservation value is still comparable to the more frequently and longer flooded lower wetland zone. The year of soil sampling was at the end of several years of high precipitation, which has resulted in a regular flooding of the upper wetland zone and a lack of farming, except for soil tillage. Thus, the seed bank might have had recovered from a prior phase of more regular farming. In semi-arid gypsum vegetation, Olano et al. (2012) observed that the soil seed bank can rapidly recover after disturbance, if the seed bank in the surrounding area is still intact. For the conservation management of such habitats this suggests that populations of rare plant species can recover, as long as flooding recurs within a certain period of time. Consequently, supporting a fluctuating hydrological regime is crucial for preserving these rare species. On the other hand, a changing climate, altering the flooding regime might lead to a further decline of temporarily flooded depressions and the related plant communities. In the Mediterranean region, predicted decrease of precipitation (IPCC, 2007) may lead to shortened hydro-periods that are likely to reduce spatial extent of the amphibious plant communities (Ghosn et al., 2010).

Species composition changes along flooding gradients

The emerging seedling communities were strongly differentiated by flooding duration, indicating that the seed bank of temporarily flooded depressions has the potential to promote different plant communities depending on the actual water regime. As increasing duration of inundation impaired the living conditions for terrestrial species and improved the establishment of water plants, the gradient from temporary to permanent flooding caused a nearly complete species turnover. Similar to field studies, which observed a clear moisture gradient in the communities of temporarily flooded depressions (Hoffmann, 1996; Altenfelder *et al.*, 2014), species composition of seed bank samples from the upper and lower wetland zone differed. This is consistent with findings of Aponte *et al.* (2010), who found a gradient in seed bank composition along a moisture gradient. Additionally, the regular water level changes, transporting hydrochourous seeds at the water surface or zoochorous dispersal by birds may contribute to this difference between the two wetland zones.

The experimental water level had no effect on the species composition, probably because flooding at any depth provides constant temperatures under which only a certain set of species is able to germinate (Pons and Schröder, 1986). It might also be that plant species react stronger to light availability which not necessarily depends on depth of the water column (Wetzel, 2001). It can be changed by the turbidity of the water as well as by shading through vegetation cover. During our experiment all ponds were mostly clear and light availability was high even at the flooding level of 40 cm. This is consistent with seed bank analyses by Casanova and Brock (2000) who found minor effects of inundation depth on species composition in Australian temporary wetlands. There, depth had an effect in separating groups under waterlogged conditions or no flooding. Among treatments with fluctuating water levels there were no effects of inundation depth as in our experiment. As the influence of flooding depth on seedling establishment might have gained greater importance in turbid water and as arable field depressions are often muddy further investigations with water samples of standardized light transmissivities would be reasonable.

Management implications

Our results suggest that the most promising approach to establish and to maintain a series of plant communities with high conservation values is to manage water level fluctuations. The most effective way to create diverse communities would be to realise the whole spectrum of flooding situations in a rotational order. According to our results, short duration of flooding leads to highest species richness, but evenness is highest under long-term flooding. Therefore, creating shallow zones around temporarily flooded depressions that can slowly dry up after flooding would benefit many plant species but prevent single competitive species to dominate. On the other hand, it is important to create adequate conditions for water plants by ensuring that flooding takes place regularly. This can be done by preventing or removing drainage of temporarily flooded depressions. Of course, the flooding regime should particularly focus the habitat requirements of the species of individual field depressions. To achieve a widespan species diversity different field depressions should be included in corresponding programs.

Beside these management treatments directly affecting the depressions, also more variable agricultural land use may improve the diversity of the ephemeral plant communities. Devictor *et al.* (2007) showed that soil tillage is an important management aspect that can enhance species richness of these plant communities. Also rare species occurring at temporarily flooded depressions are annuals and rely on regular disturbance by soil tillage (see Appendix A9). Setting aside these areas would lead to a rapid change in the species composition towards perennial communities suppressing rare plants (Hoffmann, 1996). Furthermore, more restrictive applications of herbicides and fertilizer will improve the diversity of temporarily flooded depressions (S. Altenfelder, unpubl. data). These conservation measures would provide suitable habitat conditions for different plant communities along a flooding gradient. They could enable the whole set of endangered species and rare communities to establish over a sequence of wet and dry years at the same location.

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Chapter 4

Effects of farming practice on populations of threatened amphibious plant species in temporarily flooded arable fields – implications for conservation management³

Abstract

Intensification of land use has led to a severe decline of arable plants in the past decades, particularly among species of marginal habitats, e.g. temporarily flooded fields. Few studies have focused on the factors controlling population dynamics of these species, and on suitable strategies for more effective conservation. To examine the effects of farming practice on plant populations of temporarily flooded fields we determined above-ground and below-ground densities of four annuals (Elatine alsinastrum, Limosella aquatica, Myosurus minimus, Peplis portula) in a 3-year on-farm experiment. A fully-factorial experiment combined the treatments soil tillage, crops, fertilization and herbicide application. Soil tillage had a positive effect on plant establishment, whereas herbicide application negatively affected the establishment of all study species. Plant densities were controlled by application of fertilizers and herbicides, with most significant effects on *Limosella aquatica* and *Myosurus minimus*. Soil seed densities were mainly affected by environmental factors but also tillage significantly reduced seed densities of *Elatine alsinastrum* and *Peplis portula*. Other farming practices had a minor impact. Thus, reduced management can help maintaining populations of rare amphibious plant species. The impact of different

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crops, of crop rotation and the timing of management will help developing the most appropriate management strategies for conservation of these plant species.

1. Introduction

Land use and the abiotic environment both determine species composition of plant communities in agricultural landscapes (Fried *et al.*, 2008; Pinke *et al.*, 2012). Most arable plant species are adapted to traditional farming with soil tillage in autumn or early spring, low fertilization, mechanical weeding and little seed cleaning (Burrichter *et al.*, 1993; Fried *et al.*, 2008). During the past decades, however, the arable biodiversity has experienced severe declines due to intensified land use and soil melioration (Sutcliffe and Kay, 2000; Meyer *et al.*, 2013; Sutcliffe *et al.*, 2015). This development has stimulated efforts to improve the situation for plants and animals that depend on traditional agricultural management.

Causes and consequences of the declining agro-biodiversity have been investigated in various studies (Fried *et al.*, 2009; Storkey *et al.*, 2012), with results implemented in several conservation schemes, for example, the 'field margin strip programs' (Schumacher, 1980; Marshall and Moonen, 2002), 'production integrated compensatory measures' (Litterski *et al.*, 2008), '100 fields for biodiversity' (Meyer *et al.*, 2010), and 'high nature value farmland' (PAN *et al.*, 2011; Sutcliffe *et al.*, 2015). However, a shortcoming of most conservation programs is their almost exclusive focus on plants or animals from terrestrial arable habitats, while conservation, for example, of species of temporarily flooded arable fields has been rarely addressed.

Temporarily flooded fields have a flora quite distinct from terrestrial arable habitats including numerous rare and endangered species (Hoffmann *et al.*, 2000; Bissels *et al.*, 2005; Eliáš *et al.*, 2011; Lukacs *et al.*, 2013). Plant species of these habitats naturally occur at riparian habitats of shallow lakes, ponds and rivers (Deil, 2005). As these ecosystems have experienced a steep decline due to drainage of wetlands and river regulation (e.g. Dynesius and Nilsson, 1994; Bilz *et al.*, 2011), temporarily flooded fields have become secondary habitats for the associated species. However, few studies have been published on conservation management of the respective plant communities.
Introduction

The specific vegetation of temporarily flooded fields is determined by irregular water fluctuations, by regular disturbance through tillage and weed control, and by competition with crops and common weeds. In wet years temporary abandonment of farming provides favourable conditions for amphibious plants; most of them produce large amounts of seeds that can persist in the soil seed bank for decades (Salisbury, 1970; Harper, 1987; Bossuyt and Honnay, 2008). As a persistent soil seed bank slowly responds to changing management conditions, it reflects the long-term management history of a given site (Ryan *et al.*, 2010), and acts as a buffer for periods of unfavourable management. However, little is known about specific effects of arable management on population dynamics of species occurring at temporarily flooded fields.

Timing and frequency of soil tillage, weed control and water level fluctuations determine the population dynamics of individual species. Tillage in fall favours winter annuals like Myosurus minimus that germinate right after seedbed preparation, and then flower and reproduce in spring, while tillage in spring supports summer annuals. Flooding in late winter with a water level drawdown in spring is also advantageous for summer annuals, including amphibious plants. Since herbicides mainly affect the plants at the time of application (Kleijn and van der Voort, 1997; Storkey et al., 2010), their efficacy strongly depends on treatment timing, and on species-specific germination requirements. Spraying in fall and early spring mainly affects winter annuals, while latespring application determines abundance of summer annuals. Competition is another factor influencing arable plants. Crops compete with rare species for light, thus reducing their establishment and reproduction (Epperlein et al., 2014). Fertilization increases cover of crops and of competitive weeds, while reducing germination, growth and seed production of rare arable plants through shading and nutrient competition (Bilalis et al., 2010). Hardly any study has focused on the impact of farming practices and water regime on establishment and seed banks of annual plants of temporarily flooded fields.

Here, we investigate the main factors controlling population dynamics of four annual plant species of temporarily flooded fields under different management regimes. The following hypotheses were tested in a factorial field experiment in NE Germany:

- Regular soil tillage increases establishment and reproduction of short-lived amphibious species of temporarily flooded fields.
- (ii) Herbicide applications favour late-germinating amphibious species by the removal of early-developing competitors.
- (iii) Fertilization benefits the crops and competitive weeds, thus reducing plant density and seed production of amphibious species.
- (iv) Crop competition reduces plant density and seed production of amphibious species resulting in a decline of their soil seed bank.

2. Methods

Study site

To ensure homogeneous site conditions and even land-use history, the experiment was conducted on one conventionally managed farm ('Agrar GmbH Parstein-Bölkendorf'), located in NE Germany (Federal State of Brandenburg; 53° 0'52 N, 13°59' E; 55 m a.s.l.). The moraine landscape and the fertile, alkaline luvisols with an almost neutral soil reaction are a product of glacial till deposited during the last ice age and the early holocene. Glacial sedimentation processes also left numerous kettle holes which are temporarily or permanently inundated. Depending on the permeability of the subsoil and on precipitation, the water level and also the area of these wetlands fluctuate. The region is characterized by a temperate climate with an average annual temperature of 9 °C and about 500 mm of precipitation (1981–2010; DWD, 2014). Above average precipitation in at least two subsequent years regularly leads to extensive flooding. Based on aerial photographs over 12 years (Schmidt, 1996), the inundated area varied between <1% and 15% of the study area.

Seven temporarily wet depressions spread over 60 ha were selected for the study according to the presence of the four target species. The geographical distances between these depressions were 0.2–1.0 km with a mean of 0.5 km.

Study species

Four study species were selected that have been reported occurring at temporarily flooded arable fields (Pietsch and Müller-Stoll, 1974; Albrecht, 1999; Hoffmann *et al.*, 2000; Nagy *et al.*, 2009; Popiela *et al.*, 2013). Nomenclature of species follows Wisskirchen and Haeupler (1998).

Elatine alsinastrum L. ('Whorly Waterwort', Elatinaceae) is a semi-aquatic therophyte, adapted to temporarily flooded habitats. This species has a short reproduction cycle being able to produce high amounts of persistent seeds under favourable conditions. It is distributed throughout Europe and Western Asia (Meusel *et al.*, 1978; Popiela *et al.*, 2013), being rare throughout its whole distribution range (Lansdown, 2014).

Limosella aquatica L. ('Water Mudwort', Scrophulariaceae) and *Peplis portula* L. ('Spatulaleaf Loosestrife', Lythraceae) are also summer annuals with a short life cycle adapted to semi-aquatic habitats. Like *Elatine alsinastrum* both species develop variable morphological forms, depending on the water level (Hegi, 1926; Hartl and Wagenitz, 1965). *Limosella aquatica* has its distribution range throughout the northern hemisphere except the Arctic, whereas *Peplis portula* occurs in most parts of Europe (Jäger, 2011); both species are not threatened on a global scale (Lansdown, 2014), but have been declining during the past decades and thus are considered vulnerable (*Limosella aquatica*) and near-threatened (*Peplis portula*) on a regional scale (Landesumweltamt, 2006).

Myosurus minimus L. ('Tiny Mousetail', Ranunculuaceae) is a winter annual of temporarily flooded sites that can tolerate flooding, but does not change morphologically (Conert *et al.*, 1974). Its distribution ranges from Europe to Western Asia and North America (Jäger, 2011). Due to its early flowering in spring, it is

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particularly exposed to herbicide application in arable fields (Edesi *et al.*, 2012). In the study area this species is considered near-threatened (Landesumweltamt, 2006).

Experimental design

A fully-factorial field experiment was established with and without soil tillage, crops, fertilization and herbicide application. The treatment combinations were randomly assigned to plots where the study species occurred. Together with the control plots ('no treatment') this amounts to a total number of 16 variants. Each variant was replicated six times, resulting in 96 plots per species. Due to limited occurrence of some of the study species during plot establishment in spring 2012, we decided to include plots with more than one study species, and neglected possible interactions among the small and low competitive species. In total, 178 plots were established.

The response of the study species to the different treatments was recorded on 1-m² plots that were installed in June 2012. In autumn 2012, all plots were ploughed to a depth of 20 cm to ensure equal starting conditions. In 2012, we counted the plants of each study species as a reference prior to application of the different treatments. The effects of the treatments were then evaluated in two consecutive years.

Management operations in the experimental plots were adapted to common practice on the research farm, i.e. soil tillage was done manually, simulating the use of field cultivators and disc harrow. Due to the high number of small plots which were exactly adjusted to the growing areas of the target species using machinery for soil tillage was not possible. Winter wheat (cv. 'Akteur') was sown in October 2012 and September 2013 (200 kg ha⁻¹), herbicides were sprayed in April and October 2013, and in March 2014 (broad-spectrum herbicides against dicotyledons and grasses: Flufenacet, Flurtamone, Diflufenican), and mineral NPK fertilizer (in total 160 kg N ha⁻¹) was applied at three different dates from mid-March to mid-July. Due to flooding, the application of herbicides and fertilizers was delayed in 49 plots (Table 6). Plots with delayed application of fertilizers until early August (N = 13) were considered as 'no fertilizer input' in the final analysis.

Table 6: Number of plots with treatments that had to be changed due to flooding in 2013. Depending on the duration of flooding (1, 3 or 5 months), treatments could not be applied or were delayed.

	Flooded ≥5 months	Flooded ≥3 months	Flooded ≥1 month		
Ν	13	5	31		
Crop	no emergence	no emergence	no emergence		
Fertilization	delayed	delayed	normal application		
Herbicide application	not possible	delayed	normal application		

Environmental variables

As experimental plots were established at seven different ponds with potentially different microclimatic conditions, we accounted for possible effect by pond identity in the statistical analyses. The water level of the plots was recorded every month during the vegetation period, and the observations were assigned to the categories 'flooded' or 'not flooded'. To account for potential competition, cover of all weed species was recorded in the plots once a year at the peak of vegetation cover, i.e. June 2012, July 2013 and June 2014. For the period prior to the first seed bank sampling in 2012, normal field management, i.e. soil tillage, sowing, fertilization and herbicide application was assumed, when no flooding was observed in aerial photos, taken in early May 2012 (Bing, 2012).

Sampling of the study species

Plant densities of *Elatine alsinastrum*, *Limosella aquatica*, *Myosurus minimus* and *Peplis portula* were recorded every year twice in each plot. For the early developing *Myosurus minimus*, the two sampling periods ranged from late-April to mid-May, and from mid- to late-June, depending on the start of the vegetation period in the different years (see Appendix A10). Due to later germination, the counting periods for the other species were mid- to late-June and mid-July to early-August. To avoid edge effects, only the central area (80 cm x 80 cm) of the plots was considered; for data analysis these numbers were extrapolated to 1 m².

Few plants of *Elatine alsinastrum* established in the field in 2013 (present in 16 plots) and none in 2014, most likely due to below average precipitation (Table 7). Therefore, these data were not used for data analysis. Due to an unusual drought from autumn 2013 to summer 2014, also *Limosella aquatica* and *Peplis portula* failed to establish in 2014. Thus, these field data were also excluded from further analyses.

Table 7: Accumulated precipitation and deviation on a percentage basis from the long-term average (1981–2010: 521 mm) for the study years and seasons using data from the weather station Angermünde (DWD, 2014).

		Deviation long-term mean [%]								
Year	Accumulated precipitation [mm]	Year	Winter	Spring	Summer	Fall				
2012	543	104	162	58	122	110				
2013	483	93	102	100	82	92				
2014	404	78	70	77	69	94				

Soil seed bank sampling

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To evaluate the effects of agricultural management on the seed bank, soil samples were randomly collected from each plot before the experiment started in August 2012, and after 2 years of different management treatments in August 2014. As high numbers of small samples are more suitable to detect seeds with an uneven

distribution in the soil, we took five soil corers per plot, each with a diameter of 3.3 cm and a sampling depth of 20 cm. This corresponds to the depth of soil tillage usually practiced on the study farm. Following Gruber *et al.* (2010) we assumed that regular tillage has led to an almost even seed distribution within the plough horizon.

The soil samples were transferred to 5-cm deep polystyrene trays with a size of 22 cm x 17 cm. Approximately two thirds of each tray were initially filled with autoclaved soil and then overlaid by a 2-cm layer of the soil samples. Seed bank analyses before and after the experiment ran from August 2012 until late July 2013, and from August 2014 until late July 2015. The pots were placed in a frost-protected greenhouse and kept moist during the experiment. The emerging seedlings of the study species were counted and removed regularly. Other plant species were removed as well, and the soil was mixed thoroughly two times per year when seedling emergence decreased. Seed numbers were calculated by extrapolating the numbers of seeds detected in the surface area of the soil cores to one m².

Data processing and statistical analyses

For the establishment of the four species in the field, the maximum value of both sampling dates per year was used. To describe the effects of agricultural management and water level fluctuations on plant emergence in the field plots and the seed bank samples, zero-inflated negative binomial models were calculated (Zuur *et al.*, 2009). This type of model consists of two parts: The first (binomial) part estimates the structural zeros, while the second part models the counts, some of which may also be zero, according to a negative binomial distribution.

For the binomial part in the plant density models of *Myosurus minimus* we used soil tillage and herbicide application to model the probability of individuals to establish. Weed cover was used as an additional variable as it can change the amount of light reaching the soil surface and therefore the probability of seeds to germinate. Additionally, the seed density in the soil seed bank was used in the zero model part, because it affects the probability of plants emerging. Soil tillage, crop competition,

fertilization, herbicide application, weed cover and their two-way interactions were used in the count model, since these factors contribute to the number of individuals establishing. Pond and year including their interactions were used in the count part, as well, since the population density at different locations can differ and change over time. As flooding is an important factor for the establishment of amphibious plant species and it might determine weed cover, we included flooding and the interaction between flooding and weed cover. Finally, the seed density in the soil seed bank was also used in the count model, because different seed densities might lead to different numbers of individuals emerging. For *Limosella aquatica* and *Peplis portula* the same model was used without the factor soil tillage, because the factors 'year' and 'soil tillage' were identical for these two species (no tillage in 2012 and all plots tilled in 2013).

For the soil seed bank models of all study species we used 'pond', 'year', 'soil tillage' and 'herbicide application' in the zero-inflation part of the model. Soil tillage, crop competition, fertilization and herbicide application, as well as their two-way interactions and pond and year were used as predictor variables in the count model. Because the variables 'year' and 'flooding' were identical (flooding occurred in all plots in 2012 but no plots were flooded in 2014), the latter was not included in the seed bank models. Model selection was done using AIC (Akaike Information Criterion). Significance of the reduced models was assessed with sequential likelihood-ratio tests. As these tests only provide approximated results, only results below a probability level of 0.01 were considered significant (cf. Zuur *et al.*, 2009).

All statistical analyses were performed with R 3.0.2 (R Core Team, 2013), using the packages 'Ime4' (Bates *et al.*, 2014), 'pscl' (Zeileis *et al.*, 2008), and 'Imtest' (Zeileis and Hothorn, 2002).

3. Results

In the field, median number of plants of *Myosurus minimus* was 86 \pm 98 m⁻² in 2013 and 0 \pm 0 m⁻² in 2014 (median values \pm median absolute deviation). In 2012, 33 \pm 33

plants m⁻² of *Limosella aquatica* established and 0 ± 0 in 2013. For *Peplis portula* 87 ± 86 individuals m⁻² were recorded in 2012 and 12 ± 17 in 2013 (see Appendix A11). The median numbers of seeds of *Myosurus minimus* which emerged from the seed bank samples were 351 ± 520 m⁻² in 2012 and 2105 ± 2427 m⁻² in 2014. Values for *Limosella aquatica* were 1461 ± 2167 seeds m⁻² in 2012 and 935 ± 1387 in 2014 and for *Peplis portula* 409 ± 607 seeds m⁻² in 2012 and 1169 ± 1733 in 2014. Finally, in *Elatine alsinastrum* 0 ± 0 seedlings m⁻² emerged from the 2012 samples and 234 ± 347 m⁻² from those taken in 2014 (see Appendix A12).

Effects of soil tillage, herbicides, fertilization and crop competition on plant establishment and soil seed bank

In general, soil tillage had minor effects on the establishment of the studied species. The likelihood of *Myosurus minimus* to emerge in the temporarily flooded fields increased, but tillage had no effect on the number of individuals (Table 8). Regarding the soil seed bank, the probability of detecting *Elatine alsinastrum* decreased, and a negative effect on the seed densities of *Elatine alsinastrum* and *Peplis portula* was recorded (Table 9). Soil tillage had no effect on the presence or abundance of *Myosurus minimus* or *Limosella aquatica*.

Herbicide application significantly reduced the likelihood of all species to emerge in the field (*Myosurus minimus* and *Peplis portula*, P < 0.001; *Limosella aquatica*, P < 0.01; Figure 16, Table 8). It also reduced the density of *Myosurus minimus*, but increased the number of *Limosella aquatica*. When *Myosurus minimus* grew together with crops, no such negative effects of herbicides were observed. Regarding the soil seed bank, there were no effects of herbicide application on the seed numbers of all studied species.

While fertilization alone significantly increased the density of *Limosella aquatica*, fertilization in combination with high weed cover had the opposite effect (Table 8). In the soil seed bank, no effects of fertilization on the studied species could be observed.

Competition of the standing crop had no effect on plant or seed densities of any of the study species. Weed cover decreased the plant density of *Myosurus minimus*, whereas in plots with both, crops and a high weed cover, this effect was attenuated. Similarly, the interaction of flooding and weed cover reduced this negative effect of weed cover on density of *Myosurus minimus*. Additionally, in plots with both crops and herbicides applied, the effect on density of *Myosurus minimus* was less negative than in plots without crops (Table 8). No such effects were observed for the densities of *Limosella aquatica* or *Peplis portula*.

Site-specific effects on the population dynamics of the study species

Location at different ponds had an important effect on the likelihood of all species in the seed bank and on the densities of plants in the field. In addition, interactions between year and pond significantly affected the plant densities (Table 8). Density of plants and seeds of *Limosella aquatica*, as well as the seed density of *Elatine alsinastrum* significantly changed among years.

Flooding increased plant density of *P. portula* (Table 8), but did not affect that of the other species. Weed cover slightly reduced the probability of emergence and the number of individuals of *Myosurus minimus*, in interaction with flooding, however, this effect was compensated.

Table 8: Agricultural management (soil tillage, crop competition, fertilization, herbicide application) and abiotic factors (weed cover, flooding, pond) effects on individual densities (individuals per m²) of *Myosurus minimus*, *Limosella aquatica* and *Peplis portula* in the field. Bold values indicate significance at P < 0.01.

Count model	Myosurus minimus			Li	mosella a	Peplis portula			
	Std.				Std.		Std.		
	Estimate	Error	Р	Estimate	Error	Р	Estimate	Error	Р
(Intercept)	3.487	0.921	0.000	5.551	0.541	0.000	5.932	0.475	0.000
Soil tillage	0.676	0.371	0.069						
Crop	-1.260	0.968	0.193						
Fertilizer				5.019	1.343	0.000			
Herbicide	-0.934	0.185	0.000	1.317	0.365	0.000			
Weed cover	-0.029	0.009	0.001	-0.001	0.006	0.882	-0.015	0.007	0.032
Flooding							2.604	0.897	0.004
pondS7	-0.971	1.046	0.353	-1.607	0.535	0.003	-3.447	1.026	0.001
pondS2	4.839	0.407	0.000	-2.509	0.722	0.001	-2.337	0.385	0.000
pondS3	0.756	0.470	0.108	-1.908	0.483	0.000	-0.605	0.356	0.089
pondS4	2.510	0.440	0.000	-0.087	0.546	0.873	0.844	0.639	0.187
pondS5	2.497	0.430	0.000	-0.557	0.502	0.267	0.157	0.370	0.671
pondS6	3.670	0.440	0.000	-1.972	0.466	0.000	-3.057	0.961	0.001
Year	-0.496	0.850	0.560	-4.406	0.708	0.000	-1.900	0.885	0.032
Soil tillage x Crop	-0.768	0.347	0.027						
Crop x Herbicide	0.937	0.263	0.000						
Crop x Weed cover	0.033	0.011	0.002						
Fertilizer x Weed cover				-0.078	0.020	0.000			
Weed cover x Flooding	0.034	0.013	0.007						
pondS7 x Year	4.363	1.284	0.001	-3.851	1.214	0.002	-13.889	161.067	0.931
pondS2 x Year	-0.026	0.889	0.977	-12.070	569.600	0.983	-14.472	87.962	0.869
pondS3 x Year	1.074	1.103	0.330	0.887	0.886	0.317	1.120	0.575	0.052
pondS4 x Year	-0.846	0.977	0.386	3.496	0.856	0.000	-1.735	1.293	0.180
pondS5 x Year	0.481	0.904	0.595	1.739	0.803	0.030	0.584	0.964	0.544
pondS6 x Year	-0.483	0.963	0.616	2.206	0.710	0.002	6.266	1.770	0.000
Log(theta)	0.990	0.122	0.000	0.004	0.139	0.978	-0.030	0.112	0.789

Zero-inflation model

		Std.			Std.		Std.			
	Estimate	Error	Р	Estimate	Error	Р	Estimate	Error	Р	
(Intercept)	1.508	0.986	0.126	-3.383	0.717	0.000	-3.113	0.447	0.000	
Soil tillage	-3.724	0.665	0.000							
Herbicide	3.085	0.632	0.000	2.627	0.846	0.002	2.578	0.580	0.000	
Weed cover	-0.033	0.011	0.004							



Frequency • 3 • 6 • 9 • 12



Figure 16: Changes in the probability of field emergence of the study species a) *Myosurus minimus*, b) *Limosella aquatica* and c) *Peplis portula* in relation to soil tillage, herbicide application and weed cover. The explanatory variables were chosen based on the results of the binomial (zero-inflation) model part (Table 8). The size of the circles refers to the frequency of occurrence events used in the binomial model part; for *Limosella aquatica* and *Peplis portula*, the frequency is given in the figure. *Myosurus minimus*: soil tillage P < 0.0001, weed cover P < 0.004, herbicide application P < 0.0001; *Limosella aquatica*: herbicide application P < 0.002; and *Peplis portula*: herbicide application P < 0.0001.

Count model	Myosurus minimus			Limosella aquatica			Peplis portula			Elatine alsinastrum		
	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value
(Intercept)	6.47	0.14	0.000	9.17	0.27	0.000	7.55	0.21	0.000	7.18	0.16	0.000
Soil tillage				-0.43	0.18	0.018	-0.63	0.21	0.002	-0.84	0.17	0.000
Herbicide							-0.56	0.28	0.043			
Year	0.96	0.11	0.000	-0.98	0.16	0.000	0.55	0.19	0.003	1.16	0.14	0.000
PondS2	1.57	0.17	0.000	0.95	0.33	0.004	-1.49	0.30	0.000	-1.49	0.21	0.000
PondS3	-0.18	0.26	0.500	-1.04	0.36	0.004	0.37	0.32	0.236	-1.27	0.30	0.000
PondS4	0.92	0.20	0.000	1.01	0.33	0.002	1.81	0.29	0.000	-0.12	0.23	0.601
PondS5	0.27	0.19	0.165	0.81	0.32	0.012	0.87	0.28	0.002	-1.54	0.34	0.000
PondS6	0.58	0.17	0.001	0.59	0.29	0.038	2.83	0.24	0.000	1.43	0.21	0.000
PondS7	-0.51	0.19	0.007	-1.04	0.30	0.001	0.71	0.26	0.006	-1.82	0.38	0.000
Tillage x Herbicide							0.76	0.34	0.027			
Log(theta)	0.30	0.07	0.000	-0.52	0.08	0.000	-0.28	0.08	0.000	0.17	0.10	0.085
Zero-inflation model												
	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value	Estimate	Std. Error	P-value
(Intercept)	-1.17	0.41	0.004	-0.55	0.33	0.091	-2.73	0.55	0.000	-2.61	0.50	0.000
Soil tillage							0.58	0.31	0.064	0.94	0.28	0.001
PondS2	-17.87	2311.97	0.994	-0.86	0.42	0.044	2.98	0.61	0.000	1.95	0.56	0.000
PondS3	2.59	0.54	0.000	-0.02	0.43	0.968	2.31	0.64	0.000	2.64	0.59	0.000
PondS4	-17.85	2939.69	0.995	-18.36	1840.65	0.992	-15.31	1131.13	0.989	-15.68	1099.80	0.989
PondS5	0.16	0.56	0.782	-1.36	0.49	0.005	1.46	0.64	0.023	3.38	0.61	0.000
PondS6	-0.93	0.61	0.132	-3.01	0.70	0.000	1.70	0.60	0.004	2.26	0.53	0.000
PondS7	0.10	0.55	0.855	-4.34	1.81	0.017	-1.82	1.27	0.153	3.90	0.63	0.000
Year	-1.40	0.39	0.000	0.61	0.31	0.052						

Table 9: Agricultural management (soil tillage, fertilization, herbicide application) and site (pond) effects on seed densities (seeds per m²) of *Myosurus minimus, Limosella aquatica, Peplis portula and Elatine alsinastrum* in the soil seed bank. Bold values indicate significance at P < 0.01.

4. Discussion

Effects of soil tillage and herbicides

Soil tillage, enabling light to reach deeper soil layers, can stimulate germination of buried seeds often leading to fatal germination (Baskin and Baskin, 2014). Our results regarding the soil seed bank support this observation, since the probability of *Elatine alsinastrum* to occur in the seed bank, and the seed densities of *Elatine alsinastrum* and *Peplis portula* were reduced due to soil tillage. The wrong timing of tillage, e.g. ploughing in fall, stimulating fatal germination of summer annual species, most likely has decreased seed densities in the soil. However, as long as environmental conditions allow the species to establish and to reproduce, we expect no substantial effects of soil tillage.

Herbicide application is widely used in conventional farming to reduce weed competition (Proctor, 1986; Shelke, 1987). Accordingly, our results show that herbicides decreased the probability of all study species to emerge. The individual density of Myosurus minimus was reduced by herbicide application, whereas the summer annual Limosella aquatica showed increased plant numbers. As with disturbance by soil tillage, the timing seems to determine which species are affected by herbicide application. Winter annuals like *M. minimus* are negatively affected by spraying in fall and early spring, whereas late-germinating summer annual species are scarcely affected (Albrecht, 1989). Moreover, as herbicide application eliminates established weeds at the time of application, it might even promote late-germinating species due to reduced competition. Probably by protecting the small plants from contact with the herbicides, the standing crop attenuated the negative effect of herbicide spraying on Myosurus minimus. The interactions between fertilization and herbicide application that slightly decreased the abundance of Limosella aquatica in the soil seed bank could be caused by an enhanced growth of fertilized plants going along with an increased susceptibility to herbicides.

The probability of *Myosurus minimus* to establish in the field increased with soil tillage, which might be due to reduced competition by other weeds. Additionally, this species

produces relatively large seeds, compared to the other species studied, which may enable seedlings to reach the soil surface from deeper soil layers. Grundy *et al.* (2003) showed that *Veronica hederifolia* seeds, with an approximately ten times higher seed mass than other species examined, had enough resources to reach the soil surface from depths of 8 cm.

Effects of crop competition

Epperlein et al. (2014) found that competition by common arable weeds and a crop reduced the aboveground biomass and seed production of the rare arable weed Legousia speculum-veneris. Similarly, also Lutman et al. (2011) reported a disproportional decrease of seed production in less competitive weeds under increasing crop competition. Contrary to these results we did not find such effects of the standing crop. Winter annual species might be affected less by competition in winter-sown crops as they may escape from crop competition by early development. This was shown at the community level in French arable fields by Perronne et al. (2015). In our study, close cover of competing weeds had a negative effect on the winter annual Myosurus minimus, which was attenuated by the interaction with the standing crop. On the one hand, this might be due to the more homogeneous distribution of competing weeds compared to the crops which are usually sown in rows, and therefore have a less suppressive effect on the study species (Olsen et al., 2005; Marin and Weiner, 2014). On the other hand, phenology and resource requirements of the target species are more similar to weeds than to the crop plants. Therefore, we can also expect that weed competition is much stronger than crop competition when the resource supply is limited (Connell, 1983). Furthermore, the emergence of flood-tolerating amphibious plants like Elatine alsinastrum and Peplis portula is related to hydrological conditions which negatively affect the development of crops and therefore reduce crop competition.

Effects of fertilization

Fertilization positively affects plant growth and seed production. When there is competition by crops or weeds that have better nutrient-use efficiency and are therefore growing faster, fertilization can reverse this effect and reduce the establishment of weed species (Whigham, 1984; Kleijn and van der Voort, 1997; Storkey *et al.*, 2010). This is consistent with our results on *Limosella aquatica* which was increased by fertilization but decreased when fertilization was interacting with weed cover. Considering the lateral water run-off transporting agro-chemicals towards local depressions, the nutrient-load of temporarily flooded depressions in arable fields is assumed to be generally high (Lischeid and Kalettka, 2012). In such a nutrient-rich environment, additional fertilizer input might have only marginal effects on the other study species.

Site-specific effects on abundance of the study species

Site-specific effects which were not induced by the management significantly affected the abundance of all study species in the field and in the seed bank. The temporal variability of environmental conditions, especially precipitation might result in differences in the numbers of individuals among years. Additionally, inundation may change at small spatial scales, leading to different microhabitat conditions that control establishment and reproduction of the occurring populations (James *et al.*, 2007). In our experiment, flooding had a positive effect on the abundance of *Peplis portula*. For *Myosurus minimus*, flooding attenuated the negative effect of competition by other weeds, probably because vegetation development was delayed under flooded conditions and thus, selectively benefitted the winter annual *Myosurus minimus*. Therefore, flooding seems to be an important factor not only for the population dynamics of the individual species, occurring at temporarily flooded habitats, but also for the dynamics of the whole plant communities inhabiting these sites.

5. Conclusions

To maintain viable populations of rare amphibious plant species we recommend that (i) soil tillage should be continued. This ensures that the succession in temporarily flooded field sections is kept at an initial stage with low competition of tall perennials. We expect that the positive effect of early successional stages for plant reproduction outweighs the negative effects of ploughing on the seed bank. (ii) Herbicide application should be avoided to enable the rare amphibious species to establish and to reproduce. This particularly applies for sites with winter annuals like Myosurus minimus. To control the development and spread of highly competitive weeds, a systematic monitoring of infested areas could be necessary. We suggest to limit herbicide treatments to sites where no target species occur, and to avoid applications in areas, where these species are documented. (iii) Although fertilization may positively affect some of the study species, we recommend reducing fertilizer input at temporarily flooded parts of arable fields, since these areas already have high nutrient loads. Additionally, the efficient nitrogen-use by highly competitive weeds bears the risk of reversing the positive effects of the fertilizers. (iv) As the cultivation of winter wheat did not negatively affect the establishment of the rare plants of temporarily flooded fields, arable crop cultivation should be continued to maintain the early successional stages which are essential for the survival of the rare study species. However, since other crops than winter wheat may negatively affect the rare species, such effects must be analysed in further investigations.

Overall, our results show that extensive arable cultivation is a suitable tool to combine the maintenance of early successional stages, which favour the survival of the rare amphibious species with the production of arable goods. To improve the knowledge on suitable management strategies for the threatened plants of temporarily flooded fields and to optimize the interference between species conservation and crop production, future studies should focus on the impact of other crops, crop rotations and the effects on additional species.

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Chapter 5

General discussion

Environmental conditions and land use interact in forming the habitat conditions at temporary ponds in arable fields. Both factors together have to be taken into account, if successful maintenance and conservation of the amphibious plant species and their communities is strived. The aim of this dissertation was to examine the environmental conditions and the effects of agricultural land use on plant species and communities in temporarily flooded field ponds and synthesize the results into a conservation concept. For this purpose (i) an observational field study, revealing water regime to be the most important driver of diversity and species composition, with subordinate effects of soil properties and farming practices (ii) a common garden experiment, where the water regime was manipulated to study the resulting diversity and species composition, showing that duration of flooding has a more important effect than depth of the water table and (iii) an on-farm experiment, where combined farming treatments were applied and the changes in above-ground and below-ground densities of selected species was studied, showing that most farming practices have species-specific effects. In the following, the outcomes of the three chapters regarding the studied environmental and land use effects are discussed. In the end, conclusions from these findings will be drawn and combined into a conservation concept.

Environmental conditions

In every ecosystem and habitat type a complex interaction of microclimate, soil conditions, management and biodiversity determine the habitat conditions that allow some species to emerge and establish, whereas others are excluded owing to their specific requirements. In temporary wetlands, the water regime as a complex of hydroperiod, depth and timing of flooding determines to a major extent the diversity and

species composition. Most of the other abiotic factors are influenced by the water regime or play a subordinate role for the species composition (van der Valk, 1981; Casanova and Brock, 2000).

In detail, the species composition was most decisively determined by the duration of inundation, both under field conditions, as well as in the seedling community without competition (Chapters 2 & 3). Under field conditions with competition between species, species richness and number of Isoëto-Nanojuncetea species were increased under strong water level fluctuations, i.e. at sites that experienced short-term changes between flooding, waterlogged and terrestrial conditions, whereas it was low at sites that remained unflooded (Chapter 2). As the species in the flooding experiment were allowed to react to flooding according to their physiological optima (see Putman and Wratten, 1984), species richness of the potential community, i.e. without competition, was highest under no or short-term experimental flooding (Chapter 3), as most species germinate better under terrestrial than under flooded conditions (Poschlod et al., 1999). Accordingly, Brose and Tielbörger (2005) found that reducing competition by removing biomass of a more competitive species increases the species richness. With competitive interactions in the field, no or short-term flooding favours competitive arable plants like Echinochloa crus-galli and Tripleurospermum inodorum. Both species can become very dominant, forming a dense canopy that suppresses less competitive and smaller plant species (cf. Brose and Tielbörger, 2005). Thus, a hydro-period that inhibits the establishment of these species or an appropriate management is necessary, if the successful development of amphibious plant species and their communities is desired. Rare species emerged from the seed bank under all flooding treatments (Chapter 3). However, given that several studies found rare species to have small populations (Matthies et al., 2004; Álvarez-Yépiz et al., 2011), some species may not have been detected with the limited amount of soil analysed in the present study. This is consistent with findings of Kurtz and Heinken (2011), who found more rare arable plants using seed bank activation in the field than using the seedling emergence method in the greenhouse. Furthermore, the species identities differed in the different flooding treatments. Thus, even though the absolute number of rare species was low,

this also reflects the potential for different plant communities with high conservation values to occur in the soil seed bank of these sites.

The species composition was strongly related to the hydro-period in both studies (Chapter 2 & 3). The results of Chapter 2 indicated that especially the fluctuation of water levels affects the species composition, whereas in Chapter 3 the focus was mainly on the duration of inundation and depth without fluctuations within one year. In this study, depth had no effect on the species composition, which was related to constant and suitable germination conditions (more constant temperatures, high light availability) at different depths of the water column. This is consistent with other studies where depth of the water column was secondary in temporary ponds (Casanova and Brock, 2000) and highly important in permanent water bodies (Bando *et al.*, 2015).

Apart from hydro-period and depth, timing of flooding might be an important aspect that was not studied. Several authors report that timing of inundation supports certain plant species groups (Gerritsen and Greening, 1989; Britton and Brock, 1994; Kneitel, 2014); e.g. Britton and Brock (1994) found that species richness was changed by season of inundation. Thus, timing of flooding should be additionally investigated and should be considered in managing these plant communities.

Other environmental factors like soil nutrient content had a subordinate effect on the species composition (Chapter 2). As Albrecht (1999) found Isoëto-Nanojuncetea species to have different preferences for physical and chemical soil parameters, there was no distinct effect of soil characteristics on the species composition. Landscape level effects were not examined, but several studies found that habitat area, which was related to habitat heterogeneity, increased plant species diversity (Brose, 2001; Shi *et al.*, 2010; Bosiacka and Pieńkowski, 2011). Additionally, the landscape and habitat structure in the surroundings can change species numbers in the ponds. Waldon (2012) found ponds in north-western Poland to be most species-rich, if they were located within arable fields, but surrounded by a zone of rushes or trees, whereas field ponds without this buffer strip, or ponds located in forests had lower species numbers. In

conclusion, water level fluctuations should be promoted in order to support the development of diverse amphibious plant communities. Furthermore, other environmental and landscape factors should be considered as well in managing amphibious plant communities.

Agricultural management

In modern agriculture, four main aspects of farming practices are applied in most arable systems regardless of the cultivated crop or climatic region. Soil tillage is applied to bury weed seeds in deeper soil layers where they fail to germinate (Froud-Williams *et al.*, 1984; Scopel *et al.*, 1994; Baskin and Baskin, 2014) and to improve the soil structure in order to best promote the establishment of crops. Reducing the competition by arable plants is achieved by mechanical weeding in traditional and organic farming, whereas herbicides are applied in conventional agriculture. Fertilizer is applied to improve crop yields, whether by manure or mineral fertilizer. The crop itself acts as a competitor for the arable plants, determining timing of applied farming practices, light, nutrient and water availability and thus, affecting the arable plant species establishment and reproduction success.

As the impact of these four arable management practices on amphibious plant diversity was scarcely studied before, we tested these effects in the present study. In order to keep the number of variables manageable and to be able to easily apply the findings to the study area, all management variables were treated as binary (application/ no application) and they were applied according to the usual management practices at the study farm that represent the typical integrated farming practices within the Federal State of Brandenburg (see Chapter 4).

The effects of agricultural management on diversity, species composition and population dynamics were evaluated in Chapters 2 and 4. In Chapter 2, it could be shown that herbicide application led to highest numbers of Isoëto-Nanojuncetea species. This was explained with late germination of several species in this group and

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reduced abundance of other species that have been affected by the herbicide application. This is partly consistent with the findings in Chapter 4, where individuals of Limosella aquatica were increased due to herbicide treatment. But, on the other hand, plant densities of Myosurus minimus and the probability of field emergence of Limosella aquatica, Myosurus minimus and Peplis portula were reduced. These patterns were related to direct effects on the winter annual Myosurus minimus that establishes in early spring during the time of herbicide application. The summer annual Limosella aquatica germinates well after spraying and thus, may benefit from the reduced competition of other weeds. In conclusion, the effects of herbicide application seem to be highly species-specific and depend on timing of the application and are also likely to differ between herbicides. Furthermore, the effect of herbicides also always differs, depending on weather conditions during and after application and the growth stage and cover of the weed species being treated. In general, the wide use of herbicides has led to enormous decreases of arable plant diversity and increases in the number of threatened species (Hyvönen and Salonen, 2002; Storkey et al., 2012). The findings of this study are based only on herbicide application in winter wheat. Later application of herbicides in summer crops will likely have more severe effects on summer annual species. Thus, it seems to be evident that reducing herbicide use at temporary ponds in arable fields will benefit amphibious plant species and their communities.

Fertilization and crop competition and their interactions reduced the number of I-N species compared to unfertilized and unsown sites in Chapter 2, but total species richness was highest in only crop-sown plots. Combinations of crop competition, fertilization and herbicide application, as well as crop competition and herbicide application led to lowest total species richness. Contrastingly, crop competition and fertilization had the least effect at the population level of the studied species in Chapter 4. There, fertilization increased plant densities of *Limosella aquatica*. Crop competition had only marginal effects in attenuating negative effects of weed cover and herbicide application on *Myosurus minimus*. The positive effect of the crop on the diversity, if there was no other treatment might be explained by limited competition

for resources as the strategies of crops and weeds to compete for resources might be very different. Additionally, sowing or planting crops in rows leaves space between the rows. Thus, the suppressive effect of the crop is less than with a uniform crop spacing (Olsen *et al.*, 2005; Marin and Weiner, 2014). The overall agricultural management changed the species composition only marginally, which was related to the strong impact of water level fluctuations overriding possible effects of agricultural management (Chapter 2) that can be observed in terrestrial arable plant communities (Fried *et al.*, 2008; Pinke *et al.*, 2012). In conclusion, our findings suggest that crop competition is limited at temporary ponds, as well as the negative effects of fertilization are. Thus, cultivation of crops might be continued. As stated in Chapter 4, nutrient loads in temporarily flooded depressions are usually already high and thus, resigning fertilizer input is suggested, especially to avoid competition by more competitive plant species.

The effects of soil tillage were examined only in Chapter 4, where it increased the probability of Myosurus minimus establishment in the field, but it reduced the likelihood of *Elatine alsinastrum* to occur in the seed bank and seed densities of *Elatine* alsinastrum and Peplis portula. It was concluded that soil tillage in fall may lead to fatal germination especially of summer annuals and thus reduces the densities in the soil seed bank, whereas it could increase plant numbers in the field as it reduces competition by other weeds. Regarding the effects on diversity, soil tillage can have differing effects. Bilalis et al. (2001) found weed species numbers in a no-tillage system to decrease compared to a tillage system, which they related to residues covering the soil surface and unfavourable germination conditions for annual species. Contrastingly, Demjanova et al. (2009) found the opposite in a maize cropping system in Slovakia, but there, differences were low and mainly caused by decrease in number of perennial species. Barroso et al. (2015) finally, found no differences in weed diversity, but species composition changed between different tillage systems. As arable plant communities are pioneer communities of disturbed habitats, they would undergo a succession towards climax communities. Thus, species composition changes with soil being tilled on a regular basis. Additionally, timing of tillage determines the species composition, as

summer annuals are favoured by tillage in spring, whereas winter annuals are favoured by tillage in fall (Roberts, 1984; Fried *et al.*, 2008; Meiss *et al.*, 2010). In conclusion, it is recommended to continue soil tillage, as long as the soil is dry enough to perform this treatment. This will keep the plant communities in an initial successional stage with limited competition, allowing the predominantly annual amphibious plant species to establish.

Maintaining amphibious plant species and their communities at temporary ponds in arable fields: A concept for their conservation

Biodiversity increased in historical times due to human land use (Odgaard, 1994; Berglund *et al.*, 2008; Skold *et al.*, 2010). Many plant communities adapted to management practices (Burrichter *et al.*, 1993; Fried *et al.*, 2008) and thus, conserving these species and their communities requires continuing and if necessary adapting recent management practices. Accordingly, successfully maintaining amphibious plant species with their communities requires the collaboration of nature conservation and farmers. On the one hand, conservationists are in charge of identifying appropriate habitats and/ or populations of rare species (Figure 17). This may also require monitoring efforts over several years, as dry years could prevent the rare species from germination and establishment. Consequently, at sites that are considered for conservation, the farmer has to agree on adapting the agricultural management regulations particularly in wet years, in order to allow the target species and communities to successfully establish and reproduce (Figure 18).

The main and probably not surprising finding of this thesis is that keeping environmental conditions, especially water regimes, and management practices diverse would best benefit a large set of species and communities. The younger moraine landscape of north-eastern Germany shows a pronounced heterogeneity in landscape and soil properties (Dalchow, 2005). Land consolidation and the development of large field sizes in the former German Democratic Republic favoured a more extensive use of microhabitats where water logging and wetness impeded

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efficient usage. This variability in different habitats at a small spatial scale is the ideal precondition for maintaining populations and communities of species with different and sometimes contrasting habitat requirements. As it was proofed in Chapter 3, the seed bank at the littoral zones of temporarily flooded depressions harbours the potential to create several plant communities and thus, variable water regimes will lead to a variety of plant communities. In Chapters 2 and 4, it was shown that agricultural management has differing effects on population dynamics of species as well as on the diversity and species composition of plant communities. Thus, a sophisticated agricultural management can promote a variety of different species.

The conservation practitioner's point of view

From the perspective of nature conservation, the first step would be to identify populations of rare species or to identify sites that are suitable habitats for these rare species. If a site, where rare species occur, is in a good ecological state, which means that fluctuation of water levels is possible and no drainages are present, agricultural management practices should be adapted in a way that promotes the establishment and successful reproduction of these species (Figure 17 and Figure 18). If rare species are present at a site that is in a bad ecological state, improvement of the site conditions may be considered. In Chapter 3, it could be shown that the potential of the seed bank in such habitats is promising to form amphibious plant communities in different parts along a flooding gradient at a pond. So, it is not a matter of flooding alone, but the potential for the establishment of such communities is stored in the soil, being able to develop under the appropriate conditions. The seeds of amphibious plant species can persist over long periods of time in the soil seed bank (Salisbury, 1970). Thus, it might be a valuable indirect management measure to bring excavated ponds and especially drained ponds back to their initial state in order to bring fluctuating water levels back into the system and allow the communities to develop from the seed bank. At ponds that seem to be a suitable habitat for amphibious plant species, but no rare species are emerging, it might be possible to introduce rare species as seeds or plants whether

from habitats with viable plant populations or from habitats, where removing of installed drainages is not possible. Transferring a population as seeds or plants from one habitat that is not suitable anymore to a more suitable one would save this population from going extinct. Nevertheless, the transfer of species should be limited to a small regional scale.



Figure 17: Conceptual diagram of steps to identify and maintain suitable habitats and amphibious species of temporary ponds in arable fields.

Depending on the habitat quality, i.e. is flooding and water level fluctuation possible and depending on the occurrence of rare amphibious plant species, possible steps for maintaining populations and improving habitat quality are shown.

Management implications: The farming perspective

Figure 18 displays a conceptual diagram of management adaptations and when to apply them. If no flooding occurs, the farmer can treat the sites as usual. If the sites are flooded during winter and spring, it is usually not possible to access them with heavy machinery. Thus, farming practices will be excluded until the soil is dry enough, anyways. Depending on the time, the soil has dried up to a normal condition, it is recommended to exclude sowing of crops. If they were sown in fall and did not establish, it is recommended to exclude further farming practices. If weed densities get too high an alternative weed control could be mowing at a height of 10 cm, like Berger and Pfeffer (2011) recommended. This would prevent weed species from flowering and setting seeds, but allow the target species that are usually not as high to reproduce. Additionally, mowing at this height can save amphibian animals and eventually the breed of wading birds. To avoid problematic root weed species, like Cirsium arvense and Elytrigia repens to establish highly infested areas, it might be necessary to plough or spray herbicide within such areas, but they should be checked for rare amphibious plant species beforehand. If crops established, it is recommended to monitor the sites for rare species and apply herbicides only if they are absent. If crop cover is low due to flooding, it is preferred to abandon any further management from these sites for the remaining vegetation period. Fertilization should be excluded, as the nutrient level is assumed to be already high (Lischeid and Kalettka, 2012) and weeds that are tolerant to flooding may get an advantage to the crops when fertilizer is applied. To ensure a regular disturbance, soil tillage should be performed as usual, if the soil moisture allows for it.

Like the temporary ponds, this conservation concept is quite dynamic, allowing the farmer to manage the fields regularly, as long as no flooding occurs. If this concept will be implemented in some conservation scheme like conservation easement ('Vertragsnaturschutz') or reporting the temporarily flooded depressions as ecological priority areas ('ökologische Vorrangflächen') within the Greening reform of the Common Agricultural Policy of the European Union (BMEL, 2015), the farmer could

compensate the possible yield losses due to the flooding, which might be an additional inducement from the farmers perspective to maintain these habitats with their species and plant communities. To successfully implement this conservation concept and especially to provide an incentive for the farmers to collaborate will remain a task for the nature conservation authorities.



Figure 18: Conceptual diagram of recommended farming practices.

Depending on the flooding regime and establishment of the crops in the respective year, the recommended farming practices are given.

Publications and author contributions

The following publications derive from this thesis, for each the author contributions are outlined as well.

Chapter 2

Altenfelder, S., Raabe, U., Albrecht, H., 2014. Effects of water regime and agricultural land use on diversity and species composition of vascular plants of temporary ponds in northeastern Germany. Tuexenia 34: 145-162. doi: 10.14471/2014.34.013

Author contributions: HA contributed the basic idea for the field survey. The idea for the manuscript and the design of the statistical analysis was developed by HA and myself. I conducted the field work, the statistical analyses and drafted the manuscript. All authors did literature research. HA and UR significantly contributed to restructuring the content of the manuscript and to sharpen the focus in revising the manuscript.

Chapter 3

Altenfelder, S., Schmitz, M., Poschlod, P., Kollmann, J., Albrecht, H. Managing plant species diversity under fluctuating site conditions – the case of temporarily flooded depressions. Submitted to: Wetlands Ecology and Management. doi: 10.1007/s11273-016-9490-2.

Author contributions: HA, JK and I conceived the general idea for the experiment, the statistical design and this manuscript. MS and I jointly carried out the experiment, conducted the statistical analysis and did the literature research. I drafted the manuscript. HA, JK and PP significantly improved the focus and the content of the manuscript.

Chapter 4

Altenfelder, S., Kollmann, J., Albrecht, H. Effects of farming practice on populations of threatened amphibious plant species in temporarily flooded arable fields – implications for conservation management. Agriculture, Ecosystems & Environment 222, 30-37. doi: 10.1016/j.agee.2016.02.002

Author contributions: HA developed the general idea of the experiment. All authors jointly developed the idea of the manuscript. I conducted the experiment, the statistical analyses and drafted the manuscript. HA and JK made substantial suggestions to improve the manuscript in revising it.

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Appendix

A1 Chapter 1

Seed counting of study species

In the study area near Parstein, at the littoral zone of six ponds, plants of the four study species *Elatine alsinastrum* (N = 16; 15 of them from one pond), *Limosella aquatica* (N= 20 from five ponds), *Myosurus minimus* (N= 10 from four ponds) and *Peplis portula* were collected (N = 18 from five ponds). All plants were air dried and stored dry until seed counting.

For *Myosurus minimus*, the length of the infructescence of each plant was determined and number of seeds was counted which included in total 92 infructescences. Not ripened, unhealthy or broken infructescences were not included.

For *Limosella aquatica*, the number of capsules and the number of seeds per capsule were counted which included in total 173 capsules. Not ripened or opened capsules were not included.

For *Elatine alsinastrum* and *Peplis portula*, the number of capsules of each plant was determined and then all seeds of maximum five capsules were counted and the mean number of seeds per capsule calculated.

For all species, the thousand-seed weight was determined.

Table i: Results of seed counting of the four study species. Minimum (Min), mean with standard deviation (SD) and maximum (Max) values of number of capsules/ infructescences, number of seeds per capsule/ infructescence and seed mass are given.

	Νι	mber of capsules	5/	Numb	er of seeds per ca	ipsule/	Seed mass
		infructescences			infructescence		(mg 1000
							seeds ⁻¹)
	Min	Mean ± SD	Max	Min	Mean ± SD	Max	
Elatine alsinastrum	3	16.4 ± 13.5	47	11	42.4 ± 22.6	92	15
Limosella aquatica	5	46.7 ± 61.5	233	1	68.5 ± 34.2	144	14
Myosurus minimus	1	6 ± 3	16	69	270 ± 74	474	139
Peplis portula	14	153.9 ± 173.4	557	16.8	27.2 ± 7.1	41.4	28

A2 Chapter 2

Species traits (Jäger, 2011), classification as Isoëto-Nanojuncetea species (I-N species) and assignment to phytosociological classes (Ellenberg *et al.*, 2001). NA – associated with different phytosociological classes.

	Plant growth form	Plant life span	I-N species	Phytosociological class
Agrostis stolonifera L.	Graminoid	perennial		Agrostietea
Alisma lanceolatum With.	broad-leaved herb	perennial		Phragmitetea
Alisma plantago-aquatica L. s. str.	broad-leaved herb	perennial		Phragmitetea
Alopecurus aequalis Sobol.	Graminoid	perennial		Bidentetea
Anagallis arvensis L.	broad-leaved herb	annual		Secalietea
Apera spica-venti (L.) P. Beauv.	Graminoid	annual		Secalietea
Artemisia vulgaris	broad-leaved herb	perennial		Artemisietea
Bidens cernua L.	broad-leaved herb	annual		Bidentetea
Bidens frondosa L.	broad-leaved herb	annual		Bidentetea
Bolboschoenus maritimus (L.) Palla	Graminoid	perennial		Phragmitetea
Capsella bursa-pastoris (L.) Med.	broad-leaved herb	annual		Chenopodietea
Chenopodium album L.	broad-leaved herb	annual		Chenopodietea
Chenopodium polyspermum L.	broad-leaved herb	annual		Chenopodietea
Cirsium arvense (L.) Scop.	broad-leaved herb	perennial		NA
Conyza canadensis (L.) Cronquist	broad-leaved herb	annual		Chenopodietea
Echinochloa crus-galli (L.) P. Beauv.	Graminoid	annual		NA
Elatine alsinastrum L.	broad-leaved herb	annual	х	Isoëto-Nanojuncetea
Eleocharis palustris (L.) Roem. & Schult.	Graminoid	perennial		Phragmitetea
Elymus repens (L.) Gould	Graminoid	perennial		Agropyretea
Epilobium parviflorum	broad-leaved herb	perennial		Phragmitetea
Fallopia convolvulus (L.) Å. Löve	broad-leaved herb	annual		Secalietea
Geranium dissectum L.	broad-leaved herb	annual		Chenopodietea
Gnaphalium uliginosum L.	broad-leaved herb	annual	x	Isoëto-Nanojuncetea
Juncus articulatus L.	Graminoid	perennial		Scheuchzerio-Caricetea
Juncus bufonius	Graminoid	annual	x	Isoëto-Nanojuncetea
Juncus tenageia Ehrh.	Graminoid	annual	x	Isoëto-Nanojuncetea
Leontodon autumnalis L.	broad-leaved herb	perennial		Molinio-Arrhenatheretea
Limosella aquatica L.	broad-leaved herb	annual	x	Isoëto-Nanojuncetea
Lycopus europaeus L.	broad-leaved herb	perennial		Phragmitetea
Lysimachia vulgaris L.	broad-leaved herb	perennial		NA
Matricaria recutita L.	broad-leaved herb	annual		Secalietea
Medicago lupulina L.	broad-leaved herb	annual		Festuco-Brometea
Myosotis scorpioides L.	broad-leaved herb	perennial		Molinio-Arrhenatheretea
Myosurus minimus L.	broad-leaved herb	annual		Agrostietea
Oenanthe aquatica (L.) Poir.	broad-leaved herb	annual		Phragmitetea
Papaver rhoeas L.	broad-leaved herb	annual		Secalietea
Peplis portula L.	broad-leaved herb	annual	x	Isoëto-Nanojuncetea
Persicaria amphibia (L.) Delarbre	broad-leaved herb	perennial		NA
Persicaria lapathifolia (L.) Delarbre s. l.	broad-leaved herb	annual		Bidentetea
Persicaria maculosa Grav	broad-leaved herb	annual		Chenopodietea
Persicaria minor (Huds.) Opiz	broad-leaved herb	annual		Bidentetea
Phalaris arundinacea L.	Graminoid	perennial		Phragmitetea
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Phragmites australis (Cav.) Trin. ex Steud.	Graminoid	perennial	•	Phragmitetea
Plantago major subsp. intermedia (Gilib.) Lange	broad-leaved herb	perennial	х	Agrostietea
Poa annua L.	Graminoid	annual		NA
Poa trivialis L. s. l.	Graminoid	perennial		Molinio-Arrhenatheretea
Polygonum aviculare L. (s. l.)	broad-leaved herb	annual		Plantaginetea
Potentilla supina L.	broad-leaved herb	annual	х	Bidentetea
Ranunculus sardous Crantz	broad-leaved herb	annual		Agrostietea
Ranunculus sceleratus L.	broad-leaved herb	annual		Bidentetea
Rorippa palustris (L.) Besser	broad-leaved herb	annual		Bidentetea
Rumex crispus L.	broad-leaved herb	perennial		Agrostietea
Rumex maritimus L.	broad-leaved herb	annual		Bidentetea
<i>Rumex palustris</i> Sm.	broad-leaved herb	annual		Bidentetea
Scutellaria galericulata L.	broad-leaved herb	perennial		Phragmitetea
Sonchus arvensis	broad-leaved herb	perennial		Chenopodietea
Sparganium erectum L. s. l.	Graminoid	perennial		Phragmitetea
Stellaria aquatica (L.) Scop.	broad-leaved herb	perennial		Artemisietea
Stellaria media agg.	broad-leaved herb	annual		Chenopodietea
Taraxacum officinale agg.	broad-leaved herb	perennial		NA
Trifolium campestre Schreb.	broad-leaved herb	annual		Sedo-Scleranthetea
Trifolium hybridum L.	broad-leaved herb	perennial		Agrostietea
Tripleurospermum perforatum (Mérat) Lainz	broad-leaved herb	annual		Chenopodietea
Tussilago farfara L.	broad-leaved herb	perennial		NA
Typha latifolia L.	Graminoid	perennial		Phragmitetea
Urtica dioica L. s. l.	broad-leaved herb	perennial		Artemisietea
Veronica arvensis L.	broad-leaved herb	annual		Sedo-Scleranthetea
Vicia hirsuta (L.) Gray	broad-leaved herb	annual		Secalietea
Vicia sepium L.	broad-leaved herb	perennial		NA
Viola arvensis Murray	broad-leaved herb	annual		Secalietea

A3 Chapter 2

Site parameters of all plots examined at temporary wetlands in Brandenburg. RW: latitude; HW: longitude. Abbreviations of water levels in April-July-August: ddd - drydry-dry; dwd - dry-waterlogged-dry; wfd - waterlogged-flooded-dry; fwd - floodedwaterlogged-dry; ffd - flooded-flooded-dry. Abbreviations of farming treatments: c crop planted; cf - crop and fertilizer; cfh - crop, fertilizer and herbicide; ch - crop and herbicide; f - fertilizer; fh - fertilizer and herbicide; h - herbicide; o - control. Mean L: mean Ellenberg indicator value (EIV) for light; mean F: EIV for moisture; mean N: mean EIV for nutrients. I-N species - Isoëto-Nanojuncetea species.

Row	Code	Wetland	W	×	Altitude (m a.s.l.)	Water level code	farming treatment	Cover (%)	Mean height (cm)	mean L	mean F	mean N	Total species number	l-N species number
1	Ela1	S2	52°55.92	14°01.00	53	ddd	fh	75	6	7	5.6	6.2	10	2
2	Ela10	S2	52°55.92	14°01.00	53	ddd	fh	90	5	7.1	6.3	6.5	15	1
3	Ela11	S2	52°55.92	14°01.00	53	ddd	fh	75	18	7.1	5.9	6.1	15	1
4	Ela12	S2	52°55.92	14°01.00	53	ddd	f	70	46	7.2	6.1	6.3	10	2
5	Ela13	S2	52°55.92	14°01.00	53	ddd	cf	30	47	6.9	6.1	6.1	16	1
6	Ela14	S2	52°55.92	14°01.00	53	ddd	fh	85	15	7.2	6.4	6.6	13	2
7	Ela15	S 3	52°56.35	14°01.29	58	ddd	0	35	86	7	7	6.9	12	1
8	Ela16	S 3	52°56.35	14°01.29	58	ffd	С	40	30	7.6	8.7	6.5	14	2
9	Ela17	S 3	52°56.35	14°01.29	58	ddd	cf	90	110	7.1	6.2	6.8	7	1
10	Ela18	S6	52°56.23	14°01.53	63	fwd	cf	70	61	7.5	8	5.4	13	3
11	Ela19	S2	52°55.92	14°01.00	53	ddd	cfh	75	4	7	6.3	6.6	13	4
12	Ela2	S2	52°55.92	14°01.00	53	ddd	f	80	52	7	5.7	6.4	12	3
13	Ela20	S6	52°56.23	14°01.53	63	fwd	С	75	61	7.5	8.5	5.7	15	2
14	Ela21	S6	52°56.23	14°01.53	63	fwd	cf	70	47	7.4	8.5	5.6	14	2
15	Ela22	S6	52°56.23	14°01.53	63	fwd	0	50	57	7.5	8.6	6.3	10	0
16	Ela23	S6	52°56.23	14°01.53	63	ffd	f	55	72	7.6	8.8	6.4	12	1
17	Ela24	S6	52°56.23	14°01.53	63	ffd	f	80	70	7.5	8.8	6.4	11	1
18	Ela25	S6	52°56.23	14°01.53	63	ffd	С	80	70	7.5	8.9	6.2	10	0
19	Ela26	S2	52°55.92	14°01.00	53	ddd	fh	70	14	7.3	6.1	6.3	12	1
20	Ela27	S2	52°55.92	14°01.00	53	ddd	f	85	54	7.2	5.9	6.7	11	0
21	Ela28	S2	52°55.92	14°01.00	53	ddd	fh	75	13	7.2	6.3	6.7	11	1
22	Ela29	S2	52°55.92	14°01.00	53	ddd	f	80	51	6.8	5.6	6.8	10	0
23	Ela3	S2	52°55.92	14°01.00	53	ddd	fh	55	6	7.2	6.3	6.4	14	0
24	Ela30	S6	52°56.23	14°01.53	63	ffd	cf	70	55	7.5	8.9	6.2	10	0
25	Ela31	S6	52°56.23	14°01.53	63	ffd	С	75	60	7.5	8.8	6.4	11	1

Row	Code	Wetland	RW	×	Altitude (m a.s.l.)	Water level code	farming treatment	Cover (%)	Mean height (cm)	mean L	mean F	mean N	Total species number	l-N species number
26	Ela32	S2	52°55.92	14°01.00	53	ddd	cfh	15	7	7.2	5.7	5.9	11	0
27	Ela33	S2	52°55.92	14°01.00	53	ddd	cfh	20	5	7.1	5.4	6	7	1
28	Ela34	S2	52°55.92	14°01.00	53	ddd	cfh	10	7	7.1	5.3	5.9	10	0
29	Ela35	S2	52°55.92	14°01.00	53	ddd	cf	50	66	7.3	5.1	6.3	8	2
30	Ela36	S2	52°55.92	14°01.00	53	ddd	cf	45	42	7.1	5.4	6.5	11	1
31	Ela37	S2	52°55.92	14°01.00	53	ddd	cfh	22	6	7.2	6	5.4	7	1
32	Ela38	S4	52°56.45	14°01.35	64	ddd	h	80	72	NA	NA	NA	4	1
33	Ela39	S4	52°56.45	14°01.35	64	ddd	0	75	58	7.4	6.9	6	10	0
34	Ela4	S2	52°55.92	14°01.00	53	ddd	cfh	30	8	7.1	5.9	6.3	10	0
35	Ela40	S6	52°56.23	14°01.53	63	ffd	cf	70	75	7.5	9	6.2	10	2
36	Ela41	S6	52°56.23	14°01.53	63	ffd	f	75	70	7.4	8.9	6.2	9	0
37	Ela42	S6	52°56.23	14°01.53	63	ffd	f	65	73	7.4	9.1	6	7	1
38	Ela43	S6	52°56.23	14°01.53	63	ffd	0	70	78	7.6	8.9	5.7	9	0
39	Ela44	S6	52°56.23	14°01.53	63	ffd	0	70	67	7.6	9.3	6.4	7	0
40	Ela45	S6	52°56.23	14°01.53	63	ffd	f	80	70	7.5	9	6.8	8	1
41	Ela46	S4	52°56.45	14°01.35	64	ddd	0	65	48	7	6.5	6.1	13	0
42	Ela47	S4	52°56.45	14°01.35	64	ddd	fh	75	57	7.1	6.4	5.7	10	0
43	Ela48	S4	52°56.45	14°01.35	64	ddd	ch	70	46	7.2	6.6	6.6	11	1
44	Ela49	S 3	52°56.35	14°01.29	58	ddd	fh	55	59	7.1	6	6.3	8	1
45	Ela5	S2	52°55.92	14°01.00	53	ddd	cf	45	48	7.1	6.7	6.3	11	0
46	Ela50	S6	52°56.23	14°01.53	63	fwd	С	60	51	7.5	8.3	5.7	17	0
47	Ela51	S1	52°56.07	14°01.31	55	wfd	0	75	11	7.2	7	6.4	17	0
48	Ela52	S1	52°56.07	14°01.31	55	wfd	h	40	11	7	7	5.9	9	0
49	Ela53	S1	52°56.07	14°01.31	55	wfd	f	50	12	7.1	6.7	6.5	11	0
50	Ela54	S1	52°56.07	14°01.31	55	wfd	h	35	11	7.1	7.2	6.8	9	0
51	Ela55	S1	52°56.07	14°01.31	55	dwd	0	85	18	7.1	7	5.7	17	0
52	Ela56	S1	52°56.07	14°01.31	55	dwd	f	90	19	7.2	7.1	6.1	17	0
53	Ela6	S2	52°55.92	14°01.00	53	ddd	cf	40	37	7.1	5.8	6.5	14	1
54	Ela60	S1	52°56.07	14°01.31	55	dwd	h	80	34	7.2	7.8	6.1	12	0
55	Ela61	S1	52°56.07	14°01.31	55	dwd	fh	70	37	7.3	7.3	6.1	15	0
56	Ela62	S1	52°56.07	14°01.31	55	dwd	0	70	17	7.4	7.4	6.7	15	0
57	Ela63	S1	52°56.07	14°01.31	55	dwd	h	50	13	7.3	7.4	6.3	16	0
58	Ela67	S1	52°56.07	14°01.31	55	ddd	f	25	11	6.9	6.7	6.3	13	1
59	Ela68	S1	52°56.07	14°01.31	55	ddd	fh	90	45	7	6.2	6.5	12	0
60	Ela69	S1	52°56.07	14°01.31	55	ddd	0	80	42	6.7	5.6	6.2	10	1
61	Ela7	S2	52°55.92	14°01.00	53	ddd	fh	85	7	6.9	6.2	6.4	12	0
62	Ela70	S1	52°56.07	14°01.31	55	ddd	h	60	34	7.1	6.3	6.3	8	0
63	Ela71	S4	52°56.45	14°01.35	64	ddd	h	95	40	NA	NA	NA	5	1
64	Ela72	S4	52°56.45	14°01.35	64	ddd	С	45	40	7	6.7	5.3	14	2

Row	Code	Wetland	Ж	×	Altitude (m a.s.l.)	Water level code	farming treatment	Cover (%)	Mean height (cm)	mean L	mean F	mean N	Total species number	I-N species number
65	Ela73	S4	52°56.45	14°01.35	64	ddd	cfh	60	67	7.2	6	6.2	6	2
66	Ela74	S4	52°56.45	14°01.35	64	ddd	ch	70	74	6.6	5.3	7	7	2
67	Ela75	S4	52°56.45	14°01.35	64	ddd	fh	95	89	7.1	6.4	6.3	7	1
68	Ela76	S4	52°56.45	14°01.35	64	ddd	f	70	39	6.9	6.9	6.3	12	2
69	Ela8	S2	52°55.92	14°01.00	53	ddd	f	80	44	7.2	5.7	5.8	12	5
70	Ela81	S4	52°56.45	14°01.35	64	ddd	fh	80	59	7.2	6.6	6.3	13	0
71	Ela82	S4	52°56.45	14°01.35	64	ddd	cf	70	50	7.4	7.1	5.6	14	0
72	Ela83	S4	52°56.45	14°01.35	64	ddd	С	75	47	7.3	6.5	5.6	12	1
73	Ela84	S4	52°56.45	14°01.35	64	ddd	cf	80	69	7.3	6.8	5.6	12	2
74	Ela85	S4	52°56.45	14°01.35	64	ddd	f	80	76	7.4	7	4.7	9	2
75	Ela86	S4	52°56.45	14°01.35	64	ddd	fh	75	74	7.2	6	5.6	6	4
76	Ela87	S 3	52°56.35	14°01.29	58	ddd	f	80	110	7	5	6.4	6	3
77	Ela88	S 3	52°56.35	14°01.29	58	ddd	cf	90	90	6.8	5.6	6.3	7	3
78	Ela89	S 3	52°56.35	14°01.29	58	ddd	cfh	90	64	6.7	6	6.3	6	4
79	Ela9	S2	52°55.92	14°01.00	53	ddd	f	70	41	7.5	6.3	6.6	10	1
80	Ela90	S 3	52°56.35	14°01.29	58	ddd	ch	30	54	6.7	5	6.3	6	4
81	Ela91	S 3	52°56.35	14°01.29	58	ddd	cf	85	96	6.9	4.8	6.5	8	3
82	Ela92	S 3	52°56.35	14°01.29	58	ddd	С	85	73	6.9	6	6.3	9	4
83	Ela93	S 3	52°56.35	14°01.29	58	ddd	ch	50	23	7.2	6.9	7	9	3
84	Ela94	S 3	52°56.35	14°01.29	58	ddd	С	70	95	7.3	6.3	6.9	9	3
85	Ela95	S 3	52°56.35	14°01.29	58	ddd	cfh	60	46	7	6.2	6.4	7	3
86	Ela96	S 3	52°56.35	14°01.29	58	ffd	С	45	28	7.5	8.3	7.6	10	4
87	Lim25	S6	52°56.23	14°01.53	63	ddd	h	95	42	7.5	7.4	6.5	10	4
88	Lim26	S6	52°56.23	14°01.53	63	ddd	fh	90	38	7.7	7.2	6	6	2
89	Lim27	S6	52°56.23	14°01.53	63	ddd	h	90	25	7.3	7.4	5.8	9	0
90	Lim28	S6	52°56.23	14°01.53	63	ddd	0	60	36	7.3	7.2	5.9	12	1
91	Lim29	S6	52°56.23	14°01.53	63	ddd	f	70	81	7.2	7.2	5.9	13	0
92	Lim67	S1	52°56.07	14°01.31	55	ddd	f	80	42	6.9	5.6	6.6	8	0
93	Lim68	S1	52°56.07	14°01.31	55	ddd	0	90	36	7.2	6.3	5.9	9	0
94	Lim69	S1	52°56.07	14°01.31	55	ddd	f	90	46	6.6	5.4	6.5	8	0
95	Lim70	S1	52°56.07	14°01.31	55	ddd	fh	30	32	7	6.5	6.6	9	0
96	Lim71	S1	52°56.07	14°01.31	55	ddd	cf	80	44	6.8	5.6	5.9	13	1
97	Lim72	S1	52°56.07	14°01.31	55	ddd	h	25	11	6.8	6.3	5.9	9	0
98	Lim73	S1	52°56.07	14°01.31	55	ddd	fh	45	52	7.3	6.7	5.9	17	0
99	Lim74	S1	52°56.07	14°01.31	55	ddd	f	80	52	6.9	6.1	6.1	16	0
100	Lim75	S1	52°56.07	14°01.31	55	ddd	0	55	37	7.1	6.4	6.1	11	0
101	Lim76	S1	52°56.07	14°01.31	55	ddd	h	45	29	7	6.3	6.4	12	0
102	Lim85	S5	52°56.37	14°01.53	64	ddd	С	40	56	7.1	6.9	5.7	17	0
103	Lim86	S 5	52°56.37	14°01.53	64	ddd	cfh	90	34	7	6.7	6	12	1

Row	Code	Wetland	W	×	Altitude (m a.s.l.)	Water level code	farming treatment	Cover (%)	Mean height (cm)	mean L	mean F	mean N	Total species number	I-N species number
104	Lim87	S5	52°56.37	14°01.53	64	ddd	с	70	44	7.1	7	5.8	14	1
105	Lim88	S5	52°56.37	14°01.53	64	ddd	cf	75	67	7.2	7.1	6.1	15	3
106	Lim89	S5	52°56.37	14°01.53	64	ddd	с	50	51	7.1	7	6.5	16	3
107	Lim91	S5	52°56.37	14°01.53	64	ddd	cf	75	60	7.2	7.2	6.3	15	3
108	Lim93	S5	52°56.37	14°01.53	64	ddd	f	65	43	7.1	7	6	14	1
109	Lim94	S5	52°56.37	14°01.53	64	ddd	h	80	17	7.1	6.8	6.3	14	0
110	Lim96	S5	52°56.37	14°01.53	64	ddd	о	50	13	7.1	6.8	6.9	14	1
111	Myo15	S2	52°55.92	14°01.00	53	ddd	f	75	52	7.7	5.6	6.2	9	2
112	Myo16	S2	52°55.92	14°01.00	53	ddd	fh	73	15	7.1	6	6.6	12	1
113	Myo17	S2	52°55.92	14°01.00	53	ddd	fh	75	11	7.3	6	6.5	13	1
114	Myo27	S6	52°56.23	14°01.53	63	ddd	h	90	35	7.4	7.4	6.7	9	0
115	Myo28	S6	52°56.23	14°01.53	63	ddd	fh	90	38	7.6	7.5	7.1	7	0
116	Myo29	S6	52°56.23	14°01.53	63	ddd	0	95	34	7.3	7.1	6.8	12	0
117	Myo30	S6	52°56.23	14°01.53	63	ddd	h	90	29	7.3	6.9	6.4	12	0
118	Myo31	S6	52°56.23	14°01.53	63	ddd	cf	20	52	7.1	6	6.4	14	1
119	Myo32	S6	52°56.23	14°01.53	63	ddd	С	25	51	7.1	6.5	6.8	14	1
120	Myo33	S6	52°56.23	14°01.53	63	ddd	cf	15	50	7.1	6.3	7.1	14	0
121	Myo34	S6	52°56.23	14°01.53	63	ddd	с	30	45	7	6.7	7	13	0
122	Myo35	S6	52°56.23	14°01.53	63	ddd	cf	15	50	6.8	5.4	6.4	12	0
123	Myo36	S6	52°56.23	14°01.53	63	ddd	ch	20	16	7	5.9	6.6	10	5
124	Myo37	S6	52°56.23	14°01.53	63	ddd	с	20	44	7.1	6.4	6.6	13	5
125	Myo38	S6	52°56.23	14°01.53	63	ddd	f	95	73	7.7	7.9	6.6	9	3
126	Myo39	S6	52°56.23	14°01.53	63	ddd	f	95	64	7.6	7.7	6.9	9	3
127	Myo40	S6	52°56.23	14°01.53	63	ddd	0	90	64	7.9	7.5	6.9	7	3
128	Myo41	S6	52°56.23	14°01.53	63	ddd	0	80	55	7.6	7.6	6.9	11	5
129	Myo44	S7	52°56.11	14°01.53	60	wfd	f	80	31	7.1	6.9	6.2	14	2
130	Myo45	S7	52°56.11	14°01.53	60	wfd	h	65	13	7	6.5	5.5	11	0
131	Myo46	S7	52°56.11	14°01.53	60	wfd	0	70	24	7.2	6.5	5.8	14	3
132	Myo47	S7	52°56.11	14°01.53	60	wfd	cfh	65	20	7.3	6.9	5.6	7	1
133	Myo48	S7	52°56.11	14°01.53	60	wfd	cfh	70	16	7.2	6.9	5.4	9	1
134	Myo49	S7	52°56.11	14°01.53	60	wfd	С	80	21	7.1	6.8	5.6	16	1
135	Myo50	S7	52°56.11	14°01.53	60	wfd	С	80	23	7.2	6.9	6	15	1
136	Myo51	S7	52°56.11	14°01.53	60	wfd	cfh	68	17	7.2	7	5.3	12	2
137	Myo52	S7	52°56.11	14°01.53	60	wfd	С	85	22	7.3	7.2	5.6	12	1
138	Myo53	S7	52°56.11	14°01.53	60	wfd	f	90	30	7.3	7.1	6.3	16	1
139	Myo54	S7	52°56.11	14°01.53	60	wfd	0	85	26	7.3	7.2	5.9	13	2
140	Myo55	S7	52°56.11	14°01.53	60	wfd	h	60	4	7.1	7.5	5.4	12	1
141	Myo56	S7	52°56.11	14°01.53	60	wfd	fh	45	4	7.4	7.7	5.9	9	0
142	Myo57	S7	52°56.11	14°01.53	60	wfd	0	55	13	7.2	7.3	5.6	11	4

Row	Code	Wetland	RW	MH	Altitude (m a.s.l.)	Water level code	farming treatment	Cover (%)	Mean height (cm)	mean L	mean F	mean N	Total species number	l-N species number
143	Myo58	S7	52°56.11	14°01.53	60	wfd	cfh	55	19	7.3	7.1	5.9	12	4
144	Myo59	S7	52°56.11	14°01.53	60	wfd	с	90	20	7.3	8.1	6.3	12	5
145	Myo60	S7	52°56.11	14°01.53	60	wfd	ch	70	17	7.3	7	5.9	12	3
146	Myo61	S7	52°56.11	14°01.53	60	wfd	cfh	75	17	7.3	6.9	6.2	10	5
147	Myo62	S7	52°56.11	14°01.53	60	wfd	с	90	27	7.3	6.9	6	12	5
148	Myo63	S7	52°56.11	14°01.53	60	wfd	cfh	75	15	7.1	7.2	5.4	11	3
149	Myo64	S7	52°56.11	14°01.53	60	wfd	f	85	21	7.1	7.2	6.5	18	3
150	Myo65	S7	52°56.11	14°01.53	60	wfd	0	80	34	7.1	7.3	6.1	14	3
151	Myo66	S7	52°56.11	14°01.53	60	wfd	h	60	24	7.1	7.6	6.1	14	2
152	Myo67	S7	52°56.11	14°01.53	60	wfd	fh	55	18	7.1	7.3	6	10	4
153	Myo68	S7	52°56.11	14°01.53	60	wfd	f	60	23	7.2	7.4	5.6	12	3
154	Myo69	S7	52°56.11	14°01.53	60	wfd	h	55	8	7.1	7.5	5.4	12	2
155	Myo70	S7	52°56.11	14°01.53	60	wfd	f	55	25	7.2	7.4	6.2	13	3
156	Myo73	S5	52°56.37	14°01.53	64	ddd	cf	35	64	6.8	5.4	6.3	8	5
157	Myo74	S5	52°56.37	14°01.53	64	ddd	cf	45	96	7.1	6.1	5.6	8	4
158	Myo75	S5	52°56.37	14°01.53	64	ddd	cfh	55	34	7.3	6.4	6.8	6	6
159	Myo76	S5	52°56.37	14°01.53	64	ddd	с	65	68	6.9	5.6	6.4	10	4
160	Myo77	S5	52°56.37	14°01.53	64	ddd	ch	30	11	6.9	5.8	6	7	3
161	Myo78	S5	52°56.37	14°01.53	64	ddd	ch	60	36	7.3	6.5	6.6	7	5
162	Myo79	S5	52°56.37	14°01.53	64	ddd	h	75	47	7.2	6.3	6.5	10	5
163	Myo80	S5	52°56.37	14°01.53	64	ddd	ch	60	102	6.9	6	5.9	9	2
164	Myo81	S5	52°56.37	14°01.53	64	ddd	cfh	40	84	7	5.6	6	10	2
165	Myo82	S5	52°56.37	14°01.53	64	ddd	cfh	40	93	7.2	6	6.6	11	2
166	Myo83	S5	52°56.37	14°01.53	64	ddd	fh	60	81	7	6	6.2	7	2
167	Myo84	S5	52°56.37	14°01.53	64	ddd	0	55	70	7	5.7	5.7	8	4
168	Myo85	S5	52°56.37	14°01.53	64	ddd	f	70	68	7.2	6.7	6.4	12	3
169	Myo86	S5	52°56.37	14°01.53	64	ddd	f	60	69	6.9	5.6	6	11	3
170	Myo87	S1	52°56.07	14°01.31	55	ddd	cf	75	47	6.8	6.2	6.7	8	4
171	Myo88	S1	52°56.07	14°01.31	55	ddd	ch	80	17	6.9	6.1	6.4	8	4
172	Myo91	S 3	52°56.35	14°01.29	58	ddd	fh	60	95	7.2	5.5	6.2	6	4
173	Myo92	S 3	52°56.35	14°01.29	58	ddd	f	70	73	7.1	5.2	5.6	10	5
174	Myo94	S 3	52°56.35	14°01.29	58	ddd	С	60	64	7.2	5.3	6.1	10	3
175	Myo95	S 3	52°56.35	14°01.29	58	ddd	ch	43	24	7	5.6	6.1	10	3
176	Myo96	S 3	52°56.35	14°01.29	58	ddd	ch	55	26	7.2	6.5	6.9	10	5
177	Pep53	S 3	52°56.35	14°01.29	58	ddd	h	50	18	7	5.8	6.6	6	3

A4 Chapter 2

Vegetation Relevés of all plots with water levels dry-dry-dry in April-July-August.

Column	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
	35	73	89	88	91	32	29	74	72	87	33	28	4	25	27	13	10	ო	94	96	57
Cada	Ë.	<u>.</u>	Ĩ.	Ĩ.	Ë.	Пa	Ë.	<u>.</u>	Ца.	Ĩ.	Ë.	Ë.	٨v	Ë.	Ë.	Ца	Па	Шa	Ë.	Ë.	Ela(
Agreetie stelepifere		-	-	1		4	1	1	_		_	1	2	-	1	-	4			_	-
Agrostis stolorillera	1	1	•	1		1	1	I	·		•	1	1	1	1	·	1	•	•	•	1
	1	1	I	1	1	I	I	•	·	1	I	I	I	1	1	·	I	I	I	I	1
Anayanis arvensis	•	1	•	•		•	•	I			•	·	•	•	·	·	•	·		•	1
	1	•	I	I	I	I	·	•	I	I	I	·	•	•	·	·	·	·	1	I	·
Artemisia vulgans		•		·	·	·	·		•	·									4		·
	1	•	I	•	•	·	·	I	·	•	I	I	I	I	I	I	I	I	I	I	·
Capsella bursa-pasions	·		·	•	•	·	·		·	·	·	·	•	•	·	•	·		•	•	•
Cheriopodium album	•	1	·	·	·	•	•	1	·	•	•	·	·	·	·	1	·	1	·	1	1
Cirsium arvense	•	•	·	•	•	·	·	•	·	•	·	·	•	•	·	·	•	•	·	•	·
	•		•			•	•		·	•	•		·			•	1	1		•	•
Echinochioa crus-galli	1	1	I	I	I	•	I	I	·	I	I	I	•	I	I	I	I	I	I	I	I
	•	1	•	•		1	•	·	•	•	•	·	·	·	·	·	1	·	•	•	·
Environmentation Environmentation	l '	•		1	I		•	•	1		1	•	•	•	•	·	1	•	I		•
Epilopia convolvulus	•	•	·	·	·	1	·	·	1	·	•	1	·	•	·	·	•	·	·	·	·
Coronium dissoctum	•	•	·	•	•		•	•	1	•	·	1	•	•	•	•	1	•	•	·	•
Geranium uissectum	•	•	•	•	•	•	•	•	•	•		·	•	•	·	1	1	1	•	·	·
	l '	•	1	1	•	1	•	•	1	1	1	·	•	•	·	·	•	1	I	·	·
	•		·	·	·	•	•	·	1	·	•	·	·		·	·	·	·	·	•	·
l imosella aquatica	1	1	·	1		1	1	1	1	1	1	1	·	•	1	·	·	·	1	•	1
	l '	'	•	'	•				'	1			•	•	1	•	•	•	'	•	1
Lysimachia vulgaris	•	•	•	·	•	•	•	•	•	•	•	·	•	•		1		·	·	•	
Matricaria recutita	•	•	·	·	•	•	•	•	·	•	•	·	•	•	·			·	·	•	·
Medicago Jupulina	•	•	•	•	•	•	•	1	•	•	•	•	•	•	•	•	•	•	•	•	•
Myosurus minimus	1		1	1	1	1	1		1	1		1	1			1	1	1	•		•
Oenanthe aquatica	1				1								1						•		•
Papaver rhoeas	Ċ			÷	÷								÷								
Peplis portula	1	1	1	1	1	1	1	1	1	1	1	1		1	1				1	1	
Persicaria amphibia											1					1					
Persicaria lapathifolia							1											1		1	
Persicaria maculosa		1						1													1
Persicaria minor								1													
Phalaris arundinacea			1	1	1		1				1									1	
Plantago major subsp.																					
intermedia	1	1	1		1		1	1	1	1	1	1			1	1		1	1	1	1
Poa annua	1	1	1		1		1	1					1			1	1	1	1	1	
Poa trivialis								1								1	1				1
Polygonum aviculare	1	1	1	1	1	1		1	1	1	1		1			1	1	1	1	1	
Ranunculus sardous		•	·	•									•	•		1		1	•		•
Rorippa palustris		1	1	1	1	1			1	1	1			1							1
Rumex crispus		•	·	•			1	1		•			1	1	1	1	1	·	•		•
Rumex maritimus		1	1	1	1							1	1	1					1	1	
Rumex palustris		•		·									1					·			·
Scutellaria galericulata		•		•										•					•		
Stellaria aquatica		•		•		1			1					•					•		
Stellaria media agg.	•	•		•	•	•	•	•	·	•	•	•	•	•	•		•	•	•		•
Taraxacum officinale agg.	•	•	·	·	•	·	·	•	·	•	•	·	·	1	·	·	·	·	·	·	·
Trifolium hybridum	•	•	÷	•	•	·	·	•	÷	•	•	÷	•	•	·	÷	·	÷	·	÷	1
Tripleurospermum perforatum	1	1	1	1	1	1	1	1	1	1	1	1	1	·	•	1	1	1	·	1	1
Urtica dioica	•	·	·	·	•	•	•	•	·	•	·	·	•	•	·	·	•	·	·	·	·
Veronica arvensis	•	•	•	•	•	·	·	•	·	·	·	·	·	•	·	:	·	•	·	•	•
Vicia hirsuta	:	•	;	;	•	·	:	•	;	;	·	;	·	•	·	1	·	•	;	•	•
viola arvensis	1	•	1	1	·	•	1	·	1	1	·	1	•	•	·	•	•	·	1	•	·

Column	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
	9	4	29	30	27	38	Ģ	5	4	ŝ	<u></u>			<u>6</u>	ŝ	39	~	32	17	37	ი
Code	Ela7	Ela8	Ayo	Ayo	Ayo	Ayo	Ela4	Ela8	Ela1	Ela8	Ela2	Ela7	Ela5	Ela3	Ela8	Ayo	Ela1	Jyo	٨yo	Ayo	Ela1
Agrostis stolonifera	ш	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	ш
	•	'	1	1	1	1	'	'	1	1	1	'	'	'	'	1	1	1	1	1	•
	•	•	'	'	'		•	•	'		'	•	•	•	•	'		'			•
Anara aniaa vanti	•	•	•	·	·	·	•	•	·	•	·	·	·	·	·	•	•	•	·	•	•
Apera spica-venu	1	I	I	•	·	•	I	1	·	I	•	·	·	·	·	1	I	I	·	·	·
Artemisia vulgaris	·	•	;	·	;	·	;	I	;	·	·		;	·	·	·	;	;	·	;	;
Bidens frondosa	•	•	1	·	1	·	1	·	1	·	·	1	1	·	·	·	1	1	·	1	1
Capsella bursa-pastoris	·	·	·	·	·	·	·	·	·	·	÷	·	·	·	·	·	:	1	:	1	·
Chenopodium album	•	•	•	·	·	•	•	•	·	·	1	·	·	·	·	·	1	·	1	·	·
Cirsium arvense	•	•	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1
Conyza canadensis	•	•	•	·	·	•	•	•	1	·	1	1	·	·	·	·	·	·	1	·	•
Echinochloa crus-galli	•	•	·	1	1	•	•	1	1	·	1	1	•	·	·	·	1	1	1	1	1
Elatine alsinastrum	•	•				•	•	•		•	•			•	1	•		•			
Elymus repens	1	1				1	1	1		1	·	1		1	1	1					
Epilobium parviflorum																				1	
Fallopia convolvulus		1					1		1	1		1					1	1		1	1
Geranium dissectum									1			1	1				1		1		1
Gnaphalium uliginosum					1		1			1											
Juncus articulatus																					
Juncus bufonius																					
Limosella aquatica		1													1						
Lycopus europaeus	1																				
Lysimachia vulgaris									1			1									1
Matricaria recutita											1						1				
Medicago lupulina																					
Myosurus minimus	· ·	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Oenanthe aquatica	•				'				'					'	'	'	'	'		'	
Panaver rhoeas	•	•	·	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Poplis portula	•	•	·	•	•	•	•	•	•	•	•	•	•	•	1	•	•	•	•	•	•
Pepilo portula Borojogria omnhibia	l '	1	·		·	·	·	1	·	1	·	·	·	1	1	·	·	•	·	•	•
Persicaria amprilibia	•	•	·	•	·	•	•	•	·	·	•	·	·	·	·	•	·	·	·	·	1
	•	•	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Persicaria maculosa	·	•	·	·	·	•	•	·	·	·	•	·	•	·	·	·	·	·	·	•	·
Persicaria minor	·	•	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
Phalaris arundinacea Plantago major subsp.	•	•	•	•	•	•	•	•	·	•	•	•	•	•	•	•	•	•	•	•	•
intermedia	1	1	1	1	·	1	1	1	·	1	1	·	1	1	1	·	1	1	1	1	·
Poa annua	1	•	1	1	·	•	1	1	1	1	•	·	•	1	·	·	1	1	1	·	1
Poa trivialis	1	•	·	·		•	•	·		•	1	1	·	•	•	·	•	•	•	•	1
Polygonum aviculare	1	1	1	1	•	•	1	1	1	1	1	1	•	1	1	•	1	1	1	1	1
Ranunculus sardous	•	•				•	•	•		•	•		1	•		•		•			1
Rorippa palustris	1	1	1	1				1			1	1	1	1					1		
Rumex crispus	1				1	1										1					
Rumex maritimus		1	1	1	1	1		1	1					1		1		1			
Rumex palustris						1										1					
Scutellaria galericulata																					
Stellaria aquatica	1						1														
Stellaria media agg.													1								
Taraxacum officinale agg.																				1	
Trifolium hybridum									1												
Tripleurospermum perforatum	1	1	1	1	1	1	1	1		1	1		1	1	1	1	1	1	1	1	1
Urtica dioica													1						1		
Veronica arvensis								•		•	•	•	•	•				1	•	1	
Vicia hirsuta	·	•	•	•	•	•	•	•	•	•	•	·	1	•	•	•	1	•	•	•	•
Viola arvensis	l .	•	1	1	•	•	1	•	•	•	•	·		•	•	•		1	•	1	•
		•			•	•		•	•		•	•			•		•		•		•

Column	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
	34	9	9	ω	2	35	5	ω	ω	2	28	40		33	31	Σ		16	~	2
Code	Ayo;	-im7	-im8	Ela6	Ela1	1yo	-im7	Ela2	Ela4	Ela4	Ayo;	٨v	Ela6	Ayo;	Ayo;	-im7	Ela8	Jyo	Ela2	Ela1
Agrostis stolonifera	~	1	_	ш			1	1	1	1		1	1	~	~	1	1	~	1	1
Alopecurus aegualis		1	1	1	•	1	1	1	1	•	1	1	•	1	1	•	•	1	1	1
Anagallis anyonsis	•	•	•	•	•	•	1	•	•	•	•	•	•	•	•	1	•	•	•	•
Anaganis arvensis Anera snica-venti	1	1	•	1	1	1	1	1	•	1	•	•	•	1	•		•	•	1	1
Apera spica venia Artemisia vulgaris			•				'				•	•	•		•	•	•	•		'
Ridono frondoso	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	'	•	•
Cancella hurae nestoria	•	1	•	•	•	•	1	•	•	•	•	·		·	•	·	•	·	·	I
Capsella bursa-pasions	·	•	•	•	·	•	•	•	•	•	•	•	•	•	1	•	•	•	•	•
	·	•	•	I	·	•	•	I	•	•	•	•	1	I	I	I	I	I	I	I
	·	•	•	•	·	•	•	•	•	•	•	•	1	•	•	•	•	•	•	•
	•	•	•	•	·	·	•	•	•	•	•	·	1	•	•	·	I	•	1	•
Echinochioa crus-gaili	1	1	1	1	·	·	·	1	1	1	1	•	.I	1	1	·	·	1	1	·
	•	·		·	·	;	•	·	;		·	•	•	·	·	·	·	•	•	·
Elymus repens	:	·	1	·	·	1	·	·	1	1	·	•	•	·	•	·	·	·	·	·
Epilobium parvitiorum	1	·	•	:	:	:	·	·	•	·	·	•	:	:	÷	:	:	·	·	:
Fallopia convolvulus	1	·	•	1	1	1	·	·	•	·	•	•	1	1	1	1	1	÷	·	1
Geranium dissectum	•	·	·	·	·	·	•	·	·	·	·	·	·	·	·	·	1	1	·	1
Gnaphalium uliginosum	•	1	1	•	·	•	·	•	•	•	•	·	•	•	1	•	•	·	·	•
Juncus articulatus		•	·	•	•	•	•	•	·	•	•	·	•	•	•	•	•	•	•	·
Juncus bufonius		•	·	•	•	•	•	•	·	•	•	·	•	•	•	•	•	•	•	·
Limosella aquatica		•	1	•	•	•	•	•	•	•	·	·	•		·	·	•	•		•
Lycopus europaeus		•			1	•	·		•		•	•	•		·	•		·	•	•
Lysimachia vulgaris												•								
Matricaria recutita												•	•					1		
Medicago lupulina												·								
Myosurus minimus	1			1		1		1	1	1	1	1	1	1	1	1	1	1	1	1
Oenanthe aquatica																				
Papaver rhoeas														1	1					
Peplis portula			1				1			1										
Persicaria amphibia					1										1					
Persicaria lapathifolia																				
Persicaria maculosa	1						1									1				
Persicaria minor				1																
Phalaris arundinacea			1		1	1														
Plantago major subsp.																				
Intermedia	•	1	÷	1	·	·	1	1	1	1	•	•	•	÷	÷	1	1	1	·	·
Poa annua	•	1	1	·	·	·	1	·	1	·	•	•	•	1	1	1	·	1	•	·
Poa trivialis	•	·	·	1	·	·	·	·	•	·	·	·	·	·	·	1	·	•	1	•
Polygonum aviculare	1	1	1	1	1	1	1	1	1	1	·	1	1	1	·	1	1	1	1	1
Ranunculus sardous	:	·	•	·	÷	÷	·	÷	÷	÷	÷	•	÷	·	·	·	1	÷	·	·
Rorippa palustris	1	·	·	·	1	1	•	1	1	1	1	·	1	·	·	·	·	1	·	•
Rumex crispus	•	·	•	·	·	·	·	·	•	·	÷	•	·	•	1	·	·	·	•	•
Rumex maritimus	1	·	•	·	1	·	·	·	•	·	1	1	·	1	·	·	·	·	•	•
Rumex palustris	•	·	•	·	·	·	·	·	•	·	·	1	·	1	·	·	·	·	•	•
Scutellaria galericulata		•	·	•	1	•	•	•	•	•	•	•	•	·	•	•	•	•	•	•
Stellaria aquatica		•	•	•	•	•	•	•	•	•	·	·	•		·	·	•	•		•
Stellaria media agg.	·												1				1			
Taraxacum officinale agg.	•		•		1							•	•							
Trifolium hybridum				1		1							1				1			
Tripleurospermum perforatum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Urtica dioica	.							1											1	
Veronica arvensis	1													1	1					
Vicia hirsuta	.	1														1				
Viola arvensis	1		1		1	1							1	1	1	1				

Column	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82
		_	0	80	2	e	Þ	56		2	82		4	6	79	96	4	15	0	88
Code	Ela4	Ela9	-im	, E	-im_	Ela9	Ela3	-in	Ela2	Ela3	٨y٥	Ela1	Ela3	Ela6	Myo	٨y٥	Ela9	Иyо	Ela7	٨y٥
Agrostis stolonifera	1	1		1		1	1	1	1	1	1		1		1			1		
Alopecurus aequalis		1	1	1		1		1			1				1	1	1	1	1	
Anagallis arvensis				1	1									1						
Apera spica-venti						1					1				1	1	1			1
Artemisia vulgaris		-	•		•		•	•	-	•	•	•	•	•		•		•		•
Bidens frondosa	1	-	1		-	-	-	-	-	-	-	1	-	-	-	-	-	-		1
Cansella bursa-pastoris	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	
Chenopodium album	•	1	•	•	•	•	1	•	1	•	•	1	1	1	•	•	1	1	•	·
Cirsium arvense	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	1	•	•	•	·
Convza canadensis	•	1	•	•	•	•	•	•	•	1	•	1	1	•	•	•	•	1	•	·
Echinochloa crus-galli		•	1	·	1	•	1	•	1	1	•	1	1	1	•	1	•	•	1	1
Elatino alsinastrum		•		•		•		•			•	'	'		•		•	•	1	'
Elvmus renens	•	•	•	•	•	•	•	•	1	1	1	•	•	•	1	•	•	•	•	•
Enilobium panyiflorum	•	•	•	•	•	•	•	•				•	•	•		•	•	•	•	•
Epilopia convolvulus	1	•	•	·	•	1	•	•	1	1	1	•	•	•	1	1	•	•	·	·
Coronium dissoctum	1	•	•	•	•	'	•	•	1			•	•	•	I	'	'		•	•
Chophalium uliginagum	'	'	•	·	•	·	•	•	'	•	•	1	1	•	•	•	·	•	•	•
	•	•	•	·	•	•	•	•	•	•	•	•	•	•	•	•	•	•	I	·
	•	•	·	·	•	·	•	·	•	·	·	•	·	·	·	·	·	·	·	·
	•	•	•	·	1	·	•	·	•	·	·	•	·	·	·	·	·	·	·	·
	•	•	I	·	I	·	I	·	•	·	·	•	·	·	·	·	·	·	·	·
Lycopus europaeus	•	•	·	·	•	·	•	·	•	·	·	•	·	·	·	·	·	·	·	·
Lysimachia vuigaris	•	•	•	·	•	·	•	•	•	•	•	·	•	·	•	•	•	•	·	·
	•	•	•	·	•	·	•	•	•	•	•	·	•	·	•	•	•	•	·	·
	;	;	•	·	•	·	;	•	;	;	;				;				·	•
Myosurus minimus	1	1	·	·	•	•	1	•	1	1	1	1	1	1	1	1	1	1	·	1
Denanthe aquatica	•	•	•	·	•	·	•	•	•	•	•	·	•	·	•	•	•	•	·	·
Papaver moeas	•	•	·		•	·	•	•	•	·	I	•	·	·	·	·	·	·	·	·
Pepils portula	•	•	•	1	•	·	•	1	•	•	•	·	•	·	•	•	•	•	·	·
Persicaria amprilola	•	•	•	·	•	·	•	•	•	•	•	·	•	·	•	•	•	•	·	·
Persicaria iapathitolia	•	•	•		•	•	•	·	•	·	•	·	·	·	·	·	·	·	·	·
Persicaria maculosa	•	•	1	1	•	•	•	•	•	•	·	·	·	·	•	·	·	·	·	·
Persicaria minor	•	•	·	·	•	•	•	•	•	•	·	·	·	·	•	·	·	·	·	·
Phalaris arundinacea Plantago major subsp	•	•	•	·	•	·	•	•	•	•	•	·	•	·	•	•	•	•	·	·
intermedia			1	1	1		1			1		1	1	1					1	1
Poa annua			1	1	1			1		1	1	1			1	1			1	1
Poa trivialis														1						
Polvoonum aviculare	1		1	1	1	1	1			1	1	1	1	1	1	1	1	1	1	1
Ranunculus sardous	1	1							1											
Rorippa palustris					1	1														
Rumex crispus								1												
Rumex maritimus						1											1			
Rumex palustris																				
Scutellaria galericulata																				
Stellaria aquatica																				
Stellaria media agg.		1							1					1						
Taraxacum officinale agg.											1		1							
Trifolium hybridum										1				1					1	
Tripleurospermum perforatum		1	1	1	1	1		1	1	1	1	1	1	1	1	1	1		1	1
Urtica dioica	1	1							1									1		
Veronica arvensis	.																			
Vicia hirsuta	1		-						1						-	-		1		
Viola arvensis	.					1									1		1			

Column	'074 ⁸	a75 &	85 820,	a71 98	,035 8	a36 88	,086 8	,092 06	91 97	,036 b6	,076 G	94 180,	,095 GO	a92 96	97 080,	98 98 99	99 99 69u	100 932	101 880,	102 280,
Code	My	Ĩ	Σ	Ē	Σ	Ē	Σ	Σ	Ü	Σ	Σ	Σ	Σ	Ξ	Σ	Lir	Lir	Ü	δ	Σ
Agrostis stolonifera		1	1	1		1	1				1	1						1	1	
Alopecurus aequalis			1							1						1				
Anagallis arvensis																1	1			1
Apera spica-venti	1		1		1		1		1	1	1	1	1	1	1				1	1
Artemisia vulgaris																				
Bidens frondosa																	1			
Capsella bursa-pastoris	1				1					1										
Chenopodium album					1	1	1		1		1	1				1	1	1	1	
Cirsium arvense													1	1						
Convza canadensis						1		1										1		
Echinochloa crus-galli	•	•	•	•	1	1	•	•	1	1	•	•	1	•	•	1	1	1	•	•
Elatine alsinastrum	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Elvmus repens		1		1			1	1				1		1	1					
Epilobium parviflorum	1		•			•	•	•	•	•	•	•	•		•	•	•	•	•	•
Fallopia convolvulus	•	•	•	•	1	1	•	1	1	1	1	1	1	1	•	•	•	·	•	1
Geranium dissectum	•	•	•	•	•	•	1	•	•	•	•	1	•	•	•	•	•	·	•	•
Gnaphalium uliginosum	•	•	•	•	·	•		•	•	•	•		•	•	•	•	•	•	•	•
luncus articulatus	•	•	•	•	·	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
	•	•	•	•	·	•	•	•	•	•	•	•	1	•	•	•	•	•	·	•
Limosella aquatica	•	•	•	•	·	•	•	•	•	•	•	•		•	•	•	•	•	·	•
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	·	•	•
Lysimachia vulgaris	•	•	•	•	·	•	•	•	•	•	•	•	•	•	•	•	•	•	·	•
Lysiniachia vuigans Matricaria recutita	•	·	·	·	·	1	·	•	·	·	•	•	•	·	·	·	•	•	•	·
Matricaria reculta Madicago Jupulina	•	·	•	•	·	1	·	1	•	•	•	·	•	·	·	•	•	·	•	·
	•	·	•	•	•	•	•	1	•	•	•	•	•	·	•	•	•	•	•	•
Appanthe aquatica	1	·	I	•	I	I	1	I	1	I	1	I	1	•	I	•	•	I	I	I
Denanine aqualica	•	•	•	•	·	•	·	•	•	•	•	•	•	•	•	•	•	·	·	·
Papaver moeas	•	•	•	•	·	•	·	•	•	•	•	•	•	•	•	•	•	·	·	·
Pepils portula	1	·	•	I	·	•	·	·	•	•	·	·	•	·	·	·	·	·	•	•
Persicaria amprilbia	•	·	•	•	·	•	·	·	•	•	·	·	•	·	·	·	·	·	•	•
Persicaria rapatriliolia	•	·	•	•	·	•	·	·	·	·	•	·	·	·	·	•	•	·	•	•
	•	·	•	•	·	I	·	·	•	•	·	·	•	·	·	I	I	·	•	•
Persicaria minor	•	·	•	•	·	•	·	·	·	·	•	·	·	•	•	•	•	·	•	·
Plantago major subsp. intermedia	•	1	•	•	•	•	•	1	•	•	•	•	•	1	1	1	1	•	•	•
Poa annua		1	1		1	1	1		1		1	1			1					1
Poa trivialis																				
Polygonum aviculare	1	1	1		1		1	1	1	1	1	1	1	1	1	1	1	1	1	
Ranunculus sardous																				
Rorippa palustris		1							1					1						1
Rumex crispus					1															
Rumex maritimus																				
Rumex palustris																				
Scutellaria galericulata	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	·	•	•
Stellaria aquatica	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	·	•	•
Stellaria media ann	•	•	•	•	·	•	•	•	•	•	1	•	•	•	•	•	•	•	•	1
Taraxacum officinale and	1	•	•	•	·	•	•	•	•	•		•	1	•	•	•	•	1	•	
Trifolium hybridum	•	·	•	•	·	·	1	•	•	•	•	1	1	•	1	·	•		1	•
Tripleurospermum perforatum	1	1		1	1	1	' 1	1	1	1	1		1	1	1	1	1	1	1	1
Urtica dioica						1														
Veronica arvensis					1			1		1										
Vicia hirsuta																				
Viola arvensis	.		1		1		1	1	1	1	1			1	1				1	

Column	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121 ·	122
Column	33	101	35	10	83	23	98	75 2	8	94	4 <u>6</u>	73 1	8	90 90	6	23	9	22	21	6
Code	Ela(Ela,	Ela	Myo	Myo	Ela	Ela8	Myo	Ela(Myo	Ela,	Myo	Ela	Ela	Myo	Рер	Ela	Ela	Ela	Ela
Agrostis stolonifera			1	1	1	1	1		1											
Alopecurus aegualis		1						1								1				
Anagallis arvensis																				
Apera spica-venti		1	1	1	1		1	1		1	1	1	1	1	1		1	1	1	1
Artemisia vulgaris																				
Bidens frondosa		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Capsella bursa-pastoris		1																		
Chenopodium album													1				1			
Cirsium arvense										1	1				1		1		1	
Convza canadensis	1									1										
Echinochloa crus-galli	1			1								1			÷	·		1		
Elatine alsinastrum	÷																			
Elvmus repens					1	1	1		1	1	1	1	1	1	1		1	1	1	1
Epilobium parviflorum	-	•	•	•		•	•	•		•	•	•		•	•	•	•	•	•	•
Fallonia convolvulus	1	1	1	•	•	•	•	•	•	1	1	1	1	1	1	1	1	•	1	1
Geranium dissectum				•	•	•	•	•	•				•		•	•		•	•	
Gnanhalium uliginosum	1	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	·	•	•	•
		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	·	•	•	•
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
l imosella aquatica	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Lycopus curopacus	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Matricaria recutita	•	·	•	•	•	•	•	·	•	•	•	•	•	•	•	•	•	•	•	•
Medicado Junulina	•	·	•	•	•	•	•	·	•	•	•	•	•	•	•	•	•	•	•	•
	•	·	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Opporte aquatica	'	•	•	'	1	1	•	'	·	'	·	1	·	•	'	•	·	·	•	·
Papavor rhooas	•	•	•	•	·	·	•	•	·	•	·	·	·	•	•	•	·	·	•	·
Papaver moeas	•	·	•	•	•	•	•	·	•	•	•	•	•	•	•	I	•	·	•	•
Pepils portula	•	·	•	•	•	•	1	·	I	•	•	•	•	•	•	•	•	·	•	•
Persicalia amprilbia	•	·	•	•	•	•	•	·	•	•	•	•	•	•	•	•	•	·	•	•
Porsicaria magulosa	•	•	•	•	·	·	•	•	·	•	·	·	·	•	•	•	·	·	•	·
Persicalia maculosa	•	•	•	•	·	·	•	•	·	•	·	·	·	•	•	•	·	·	•	·
Persicana minor Phalaris arundinacoa	•	•	•	•	•	•	•	·	•	•	•	•	•	•	•	·	•	·	•	•
Plantago major subsp. intermedia			•	•	•	•	•	•	•	•	•	•	•	•	•		•	•		
Poa annua	1				1	1	1	1										1		
Poa trivialis																				
Polygonum aviculare	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Ranunculus sardous																				
Rorippa palustris		1																		
Rumex crispus																				
Rumex maritimus			1																	
Rumex palustris																				
Scutellaria galericulata											1		1	1						
Stellaria aquatica																				
Stellaria media agg.																				
Taraxacum officinale agg.										1										
Trifolium hvbridum										1										
Tripleurospermum perforatum		1	1	1				1		1	1	1	1			1	1	1	1	1
Urtica dioica																				
Veronica arvensis																				
Vicia hirsuta																				
Viola arvensis	.		1	1	1	1						1		1		1	1	1		1

Only once: 11: Sonchus arvensis 14: Chenopodium polyspermum 21: Vicia sepium 47: Tussilago farfara 61: Phragmites australis 80: Leontodon autumnalis.

A5 Chapter 2

Vegetation Relevés of all plots with water levels dry-waterlogged-dry in April-July-August.

Column	1	2	3	4	5	6
Code	Ela56	Ela55	Ela63	Ela61	Ela62	Ela60
Agrostis stolonifera	1	1			1	
Alisma lanceolatum		1	1	1		1
Alopecurus aequalis	1	1	1	1	1	
Anagallis arvensis	1	1				
Bidens cernua	1		1	1	1	1
Chenopodium album		1		1		
Echinochloa crus-galli	1	1	1	1	1	1
Elatine alsinastrum	1	1	1	1	1	1
Epilobium parviflorum	1	1				
Gnaphalium uliginosum	1	1	1			
Juncus bufonius	1	1	1			
Lycopus europaeus	1	1	1	1		1
Oenanthe aquatica				1	1	1
Peplis portula	1	1	1	1	1	1
Persicaria maculosa	1	1	1	1	1	
Persicaria minor					1	1
<i>Plantago major</i> subsp.						
intermedia	1	1	1	1	1	1
Polygonum aviculare	1		1	1	1	1
Rorippa palustris	1		1	1	1	1
Tripleurospermum perforatum	1	1	1		1	1
Urtica dioica	1				1	

Only once: 1: *Poa trivialis, Sonchus arvensis.* 4: *Juncus articulatus, Taraxacum officinale.* 5: *Rumex maritimus.*

A6 Chapter 2

Vegetation Relevés of all plots with water levels flooded-waterlogged-dry in April-July-August.

Column	1	2	3	4	5
Code	Ela50	Ela20	Ela21	Ela18	Ela22
Alisma lanceolatum	1	1	1	1	1
Alisma plantago-aquatica	1	1	1	1	1
Alopecurus aequalis	1	1	1	1	1
Elatine alsinastrum	1		1	1	
Juncus tenageia	1	1	1		
Limosella aquatica	1	1	1	1	1
Myosotis scorpioides	1	1	1	1	
Myosurus minimus	1	1		1	
Oenanthe aquatica	1	1	1	1	
Peplis portula	1	1	1	1	1
Plantago major subsp. intermedia	1	1	1	1	1
Polygonum aviculare	1			1	
Rorippa palustris		1	1		1
Rumex crispus	1	1	1	1	
Rumex palustris			1		1
Sparganium erectum	1	1	1		
Typha latifolia		1			1

Only once: 1: Cirsium arvense. 2: Eleocharis palustris. 4: Stellaria aquatica. 5: Bolboschoenus maritimus, Epilobium parviflorum, Ranunculus sceleratus.

A7 Chapter 2

Chenopodium polyspermum. July-August. Only once: 1: Cirsium arvense. 11: Juncus tenageia. 14: Elymus repens. 25: Vegetation Relevés of all plots with water levels waterlogged-flooded-dry in April-

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Column	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
	yo64	yo53	y049	y066	a51	yo50	y065	yo54	yo70	yo51	yo59	yo44	y055	y069	y068	yo52	yo60	yo46	yo58	y062	y063	y057	y045	y067	yo56	a53	yo61	a54	yo48	a52	y047
Code	Σ́	Ź	Σ́	Ź	Ш	Ź	Σ́	Σ́	Ź	Ś	Ś	Ź	Ź	Σ́	Ś	Ź	Ś	Σ́	Ź	Ź	Ź	Ź	Σ́	Ź	Σ́	Ш	Ź	Ш	Ś	Ш	Σ́
Agrostis stolonifera	•	1	•	•	·		•	•	•	1	•	1	•	•	•	•	1	•	1	1	·	1	•	•	1	•	•	•	1	•	1
Alisma lanceolatum	•	•	•		•	•	•	•	•	•	1	•	1	1	1	•	•	•	1	•	1	1	•	•	1	•	•	•		1	•
Alisma plantago-aquatica	1	•	•	1	•	•	1	•	1	•	1	•	1	1		•	1	•	•	•	•		•	1	1	•	•	•		•	•
Alopecurus aequalis	1	1	•	•	1	1	•	1	1	•	1	1	•	•		1	1	1	1	1	•		•	•	1	•	1	•		•	•
Anagallis arvensis	1				1	1	•					1						1					1								
Bidens cernua	•				1		•																			1		1			
Bidens frondosa	1	1	1	1	1	1	1	1	1	1	1	1			1	1	1	1	1	1	1	1	1	1			1		1		1
Echinochloa crus-galli	1	1	1	1	1	1	1			1	1	1	1	1			1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Elatine alsinastrum					1																							1		1	
Epilobium parviflorum	1	1	1	1		1	1				1	1			1	1		1				1									
Gnaphalium uliginosum			1	1	1			1		1			1	1			1				1		1			1		1			
Juncus bufonius		1	1		1	1				1		1	1	1		1	1	1					1			1		1	1	1	
Limosella aquatica	1		1	1			1	1	1	1	1		1	1	1	1			1	1	1	1		1	1		1		1		1
Myosurus minimus	1	1	1	1		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1		1		1
Peplis portula	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1		1
Persicaria lapathifolia			1						1			1											1								
Persicaria maculosa					1																					1		1			
<i>Plantago major</i> subsp.																															
intermedia	1	1	1	1	1	1	1	1	1	1		•	1	1	1	1	1	1		1	1		1	1		•				1	•
Poa annua	1	1	1	1	1	1	1	1	1	1		1	1	1	1	1	1	1	1	1	1	•	1	1	1	1	1	1	1	1	1
Polygonum aviculare	1	1	1		1	1	1	1	1	•		1		•	1	1	1	1	1	1		1	•	•	•	1	1			1	
Potentilla supina	1			1			1	1		1																	1				
Rorippa palustris	1	1	1	1	1	1		1	1				1	1	1					1		1		1		1		1		1	
Rumex crispus	1	1	1			1	1	1	1	1	1	1			1	1		1	1		1										
Rumex maritimus	1	1		1	1		1				1															1		1			
Trifolium campestre			1															1					1								
Tripleurospermum																															
perforatum	1	1	1	1	1	1	1	1	1	·	1	1	1	1	1	1	•	1	1	1	1	1	·	1	•	1	1	·	1	1	·

A8 Chapter 2

Vegetation Relevés of all plots with water levels flooded-flooded-dry in April-July-August.

Column	1	2	3	4	5	6	7	8	9	10	11	12	13
	Ela16	Ela23	Ela24	Ela31	Ela40	Ela25	Ela30	Ela41	Ela43	Ela96	Ela45	Ela42	Ela44
Code			ш	ш	ш	ш		ш		ш			
Agrostis stolonifera									1		1		
Alisma lanceolatum	1	1	1	1	1	1	1	1	1		1	1	1
Alisma plantago-aquatica	1	1	1	1	1	1	1	1	1	1	1	1	1
Alopecurus aequalis	1	1	1	1	1	1	1	1	1	1	1	1	1
Bidens cernua	1									1			
Bidens frondosa	1									1			
Elatine alsinastrum	1				1				1				
Eleocharis palustris	1	1											
Myosotis scorpioides			1	1	1	1	1	1	1			1	
Oenanthe aquatica	1		1	1	1	1	1	1	1	1	1	1	1
Peplis portula	1	1	1	1	1	1	1	1	1			1	1
Persicaria amphibia	1		1	1		1	1			1			
Polygonum aviculare	1									1			
Rorippa palustris		1	1	1	1					1			
Rumex crispus			1	1		1	1	1			1		
Rumex maritimus	1	1								1			
Rumex palustris		1	1	1	1	1	1	1			1		1
Sparganium erectum			1	1	1	1	1	1	1		1	1	1

Only once: 1: *Lycopus europaeus, Scutellaria galericulata*. 2: *Phalaris arundinacea*. 3: *Epilobium parviflorum, Limosella aquatica, Plantago major* subsp. *intermedia, Typha latifolia*.

A9 Chapter 3

All plant species that emerged during the experimental seed bank analysis in wet field depressions in NE Germany. Abbreviations used in the ordination plots, conservation status according to the Red Lists of Brandenburg (Kabus and Mauersberger 2011, Landesumweltamt 2006) and the life span according to the LEDA traitbase and, if no data available according to Ellenberg et al. 2001. All charophytes were considered to have an annual life cycle. Red List status: 1, critically endangered; 2, endangered; 3, vulnerable; V, near-threatened; C, common; D, data deficient.

Species name	Abbreviation	Red List status	Life span		
Agrostis stolonifera L.	Agrostol	С	perennial		
Alisma plantago-aquatica agg.	Alisagg	С	perennial		
Alopecurus aequalis Sobol.	Alopaequ	С	perennial		
Anagallis arvensis L.	Anagarve	С	annual		
Anthemis arvensis L.	Antharve	С	annual		
Arabidopsis thaliana (L.) Heynh.	Arabthal	С	annual		
Bidens cernua L.	Bidecern	С	annual		
Bidens tripartita L.	Bidetrip	С	annual		
Bolboschoenus maritimus (L.) Palla	Bolbmari	С	perennial		
Butomus umbellatus L.	Butoumbe	V	perennial		
Cerastium holosteoides Fr.	Ceraholo	С	annual		
Chara globularis Thuill.	Charglob	С	annual		
Chenopodium album L.	Chenalbu	С	annual		
Chenopodium polyspermum L.	Chenpoly	С	annual		
Cirsium arvense (L.) Scop.	Cirsarve	С	perennial		
Conyza canadensis (L.) Cronquist	Conycana	С	annual		
Echinochloa crus-galli (L.) P. Beauv.	Echigall	С	annual		
Elatine alsinastrum L.	Elatalsi	2	annual		
Fallopia convolvulus (L.) Å. Löve	Fallconv	С	annual		
Galium palustre agg.	Galiagg	V	perennial		
Geranium pusillum Burm.f.	Gerapusi	С	annual		
Gnaphalium uliginosum L.	Gnapulig	С	annual		
Iris pseudacorus L.	Irispseu	С	perennial		
Juncus articulatus L.	Juncarti	С	perennial		
Juncus bufonius L.	Juncbufo	С	annual		
Juncus tenageia Ehrh.	Junctena	2	annual		
Limosella aquatica L.	Limoaqua	3	annual		
Species name	Abbreviation	Red List status	Life span		
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Lycopus europaeus L.	Lycoeuro	С	perennial		
Matricaria recutita L.	Matrrecu	С	annual		
Mentha arvensis L.	Mentarve	С	perennial		
Stellaria aquatica (L.) Scop.	Stelaqua	С	annual		
Myosurus minimus L.	Myosmini	V	annual		
Nitella mucronata (A.Braun) Miquel	Nitemucr	С	annual		
<i>Oenanthe aquatica</i> (L.) Poir.	Oenaaqua	С	annual		
Peplis portula L.	Peplport	V	annual		
Persicaria amphibia (L.) Delarbre	Persamph	С	perennial		
Persicaria lapathifolia (L.) Delarbre s. l.	Perslapa	С	annual		
Persicaria maculosa Gray	Persmacu	С	annual		
Persicaria minor (Huds.) Opiz	Persmino	С	annual		
Persicaria dubia (Stein) Fourr.	Persdubi	D	annual		
Phalaris arundinacea L.	Phalarun	С	perennial		
Plantago major ssp. intermedia (Gilib.) Lange	Planinte	С	annual		
Poa annua L.	Poaannu	С	annual		
Poa trivialis L. s. l.	Poatriv	С	perennial		
Polygonum aviculare agg.	Polyagg	С	annual		
Potentilla supina L.	Potesupi	3	annual		
Ranunculus sceleratus L.	Ranuscel	С	annual		
Rorippa palustris (L.) Besser	Roripalu	С	annual		
Rumex crispus L.	Rumecris	С	annual		
Rumex maritimus L.	Rumemari	С	annual		
Rumex obtusifolius L.	Rumeobtu	С	perennial		
Senecio vulgaris L.	Senevulg	С	annual		
Sparganium erectum L. s. l.	Sparerec	С	perennial		
Stellaria media agg.	Stelagg	С	annual		
Symphytum officinale agg.	Sympagg	С	perennial		
Tolypella prolifera (Ziz ex A. Braun) Leonh.	Tolyprol	1	annual		
Trifolium repens L.	Trifrepe	С	perennial		
Tripleurospermum perforatum (Mérat) Lainz	Tripperf	С	annual		
Typha latifolia L.	Typhlati	С	perennial		
Urtica dioica L. s. l.	Urtidioi	С	perennial		
<i>Veronica</i> sp.	Verosp	С	NA		
Vicia tetrasperma (L.) Schreb.	Vicitetr	С	annual		
Viola arvensis Murray	Violarve	С	annual		

A10 Chapter 4

Climate diagrams of the study years using climate data from Angermünde, the next town to the study area, showing mean monthly temperature and monthly amount of precipitation. Data source: Deutscher Wetterdienst (DWD, 2014).



A11 Chapter 4

Number of plots (N), median and median absolute deviation (mad) of plant densities m⁻² of the study species in relation to farming practices, flooding, study year and pond.

	My	Myosurus minimus			Limosella aquatica			Peplis portula		
	Ν	median	mad	Ν	median	mad	Ν	median	mad	
Tillage	16	100	113	12	0	0	15	22	33	
Herbicide	6	0	0							
Crop	6	90	122							
Fertilizer	6	39	41							
Tillage x herbicide	13	3	4	14	4	6	14	0	0	
Tillage x crop	15	102	101	14	1	1	14	128	182	
Tillage x fertilizer	22	89	113	14	1	1	17	16	24	
Crop x herbicide	6	0	0							
Crop x fertilizer	5	123	111							
Fertilizer x herbicide	6	0	0							
Tillage x crop x herbicide	15	23	34	6	0	0	5	0	0	
Tillage x crop x fertilizer	16	155	207	10	2	3	9	25	37	
Tillage x fertilizer x herbicide	22	67	99	12	0	0	12	2	3	
Crop x fertilizer x herbicide	7	0	0							
Tillage x crop x fertilizer x herbicide	23	41	61	11	3	4	10	250	370	
No treatment	6	12	17	87	33	33	96	87	86	
Flooded	27	28	25	81	22	30	109	94	108	
Not flooded	163	52	77	99	3	4	83	11	16	
Year 2012				87	33	33	96	87	86	
Year 2013	96	86	98	93	0	0	96	12	17	
Year 2014	94	0	0							
Pond S1	8	3	4	16	45	67	46	48	70	
Pond S2	44	383	567	30	2	3	12	1	1	
Pond S3	12	9	13	6	3	4	22	3	4	
Pond S4	14	55	77	34	6	8	32	101	138	
Pond S5	28	62	56	21	58	86	6	106	131	
Pond S6	30	89	132	25	9	13	32	86	92	
Pond S7	54	24	36	48	13	10	42	140	156	
Total	190	44	64	180	11	16	192	60	89	

	Ν	Myosurus ı	minimus	Limosella aquatica		Peplis portula		Elatine alsinastrum	
		median	mad	median	mad	median	mad	median	mad
Tillage	119	351	520	1286	1733	468	693	0	0
Herbicide	12	1286	1560	1286	1213	2105	3120	117	173
Crop	13	2105	1387	1403	2080	3040	4160	234	347
Fertilizer	12	2455	1733	1052	1040	1637	2427	585	867
Tillage x herbicide	11	3741	4854	468	693	234	347	0	0
Tillage x crop	8	2105	2947	818	867	468	693	351	520
Tillage x fertilizer	12	818	1213	818	1213	585	867	0	0
Crop x herbicide	10	1520	1907	1052	1560	2338	2427	234	347
Crop x fertilizer	12	1988	2947	702	1040	1052	1560	0	0
Fertilizer x herbicide	9	2338	3120	935	1040	702	1040	0	0
Tillage x crop x herbicide	11	2105	2080	702	1040	935	1387	0	0
Tillage x fertilizer x herbicide	11	1169	1387	468	693	468	693	234	347
Tillage x crop x fertilizer	9	2572	2427	4443	5200	935	1387	234	347
Crop x fertilizer x herbicide	11	1871	2080	702	1040	3274	3814	234	347
Tillage x crop x fertilizer x herbicide	12	1520	1560	935	693	2806	2600	117	173
No treatment	82	935	1213	1169	1733	351	520	234	347
Year 2012	178	351	520	1461	2167	409	607	0	0
Year 2014	176	2105	2427	935	1387	1169	1733	234	347
Pond S1	52	468	433	234	347	1052	1213	1169	1300
Pond S2	55	3508	2427	468	693	0	0	117	173
Pond S3	41	0	0	117	173	0	0	0	0
Pond S4	34	1461	1647	9880	7107	7483	7627	760	780
Pond S5	46	468	693	935	1387	702	1040	0	0
Pond S6	72	1461	1300	3157	4334	234	347	0	0
Pond S16	54	351	520	1169	1040	2338	2427	0	0
Total	354	877	1127	1169	1733	702	1040	117	173

Appendix

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A12 Chapter 4