THE INFLUENCE OF TRADITIONAL FLOOD IRRIGATION ON BIODIVERSITY, PLANT FUNCTIONAL COMPOSITION AND PLANT NUTRIENT AVAILABILITY IN CENTRAL EUROPEAN GRASSLAND

by

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CONTENTS

ABSTRACT

Grassland management has been increasingly intensified throughout centuries since mankind started to control and modify the landscape. Species communities were always shaped alongside management changes leading to huge alterations in species richness and diversity up to the point where land use intensity exceeded the threshold. Since then biodiversity became increasingly lost. Today, global biodiversity and especially grassland biodiversity is pushed beyond its boundaries. Policymakers and conservationists seek for management options which fulfill the requirements of agronomic interests as well as biodiversity conservation alongside with the maintenance of ecosystem processes. However, there is and will always be a trade-off. Earlier in history, natural circumstances in a landscape mainly determined regionally adapted land use. These regional adaptions shaped islands for many specialist species, and thus diverse species communities, favoring the establishment of a high β-diversity. With the raising food demand, these regional and traditional management regimes became widely unprofitable, and the invention of mineral fertilizers ultimately led to a wide homogenization of grassland management and, as follows, the loss of biotic heterogeneity. In the course of the green revolution, this immediate coherence and the dependency between grassland biodiversity and traditional land use practices becomes increasingly noticed. Indeed, some traditional forms of management such as meadow irrigation have been preserved in a few regions and thus give us the opportunity to directly investigate their long-term relevance for the species communities and ecosystem processes. Traditional meadow irrigation was a common management practice to improve productivity in lowland, but also alpine hay meadows throughout Europe until the 20th century. Nowadays, meadow irrigation is only practiced as a relic in a few remnant areas. In parts of the Queichwiesen meadows flood irrigation goes back to the Middle Ages, which makes them a predestined as a model region to study the long- and short-term effects of lowland meadow irrigation on the biodiversity and ecosystem processes. Our study pointed out the conservation value of traditional meadow irrigation for the preservation of local species communities as well as the plant diversity at the landscape scale. The structurally more complex irrigated meadows lead to the assumption of a higher arthropod diversity (Orthodoptera, Carabidae, Araneae), which could not be detected. However, irrigated meadows are a significant habitat for moisture dependent arthropod species. In the light of the agronomic potential, flood irrigation could be a way to at least reduce fertilizer costs to a certain degree and possibly prevent overfertilization pulses which are necessarily hazardous to non-target ecosystems. Still, the reestablishment of flood irrigation in formerly irrigated meadows, or even the establishment of new irrigation systems needs ecological and economic evaluation dependent on regional circumstances and specific species communities, at which this study could serve as a reference point.

ZUSAMMENFASSUNG

Grünland in Europa wurde über die Jahrhunderte hinweg durch steigende Intensivierung der Landnutzung geprägt. Die agrarischen Veränderungen und Weiterentwicklungen formten und veränderten die Biodiversität und führten letztlich zu massivem Artenrückgang. Heutzutage ist davon auszugehen, dass die planetare Belastungsgrenze für die globale Biodiversität und insbesondere die Biodiversität von Grünland bereits erreicht wurde. Politische Entscheidungsträger und Umweltschützer suchen daher Maßnahmen, die den agrarökonomischen Zweck der Biomasseproduktion mit dem Schutz und Erhalt von Biodiversität sowie der Aufrechterhaltung von Ökosystemprozessen vereinen. In früheren Zeiten und insbesondere vor der Einführung mineralischer Stickstoffdünger war Landnutzung im Wesentlichen von den strukturellen Gegebenheiten der Landschaft abhängig. Die Entwicklung regionalspezifischer Bewirtschaftungsmaßnahmen förderte durch die Schaffung von Habitaten für speziell angepasste Arten und Artenzusammensetzungen eine hohe Diversität auf Landschaftsebene.

Staubewässerung war seit dem frühen Mittelalter bis ins 20. Jahrhundert eine europaweit verbreitete Bewirtschaftungsmaßnahme zur Ertragssteigerung. Diese Form der Bewässerung, bei der angrenzende Flüsse systematisch aufgestaut werden, um das Wasser in die Wiesen zu leiten und durch im Wasser geführte Sedimente einen Düngeeffekt hervorzurufen, war typisch für Wiesenbewirtschaftung im Flachland. Abhängig von den strukturellen Gegebenheiten wurden regionaltypische Abwandlungen der Bewässerungssysteme entwickelt und prägten somit die Flora und Fauna dieser sogenannten Wässerwiesen. Mineralische Dünger machten diese arbeitsintensive Bewirtschaftungsform weitestgehend unprofitabel, sodass diese heutzutage nur noch in wenigen Regionen reliktartig als Tradition erhalten blieb.

In den Queichwiesen nahe Landau in der Pfalz wird mit zwischenzeitlichen Unterbrechungen seit dem 15. Jahrhundert traditionelle Staubewässerung betrieben. Die vorliegende Studie nutzte die Queichwiesen als Modellregion, um sowohl Langzeit- als auch Kurzzeiteffekte der Staubewässerung auf die Biodiversität und Nährstoffverfügbarkeit zu untersuchen. In einer umfassenden Vegetationskartierung konnten wir einen positiven Effekt der Bewässerung auf die Diversität sowohl auf lokaler als auch auf Landschaftsebene verzeichnen. Eine höhere strukturelle Vielfalt durch die Förderung niedrigwüchsiger Arten legt zwar einen positiven Effekt auf die Diversität von Arthropoden (Orthodoptera, Carabidae, Spinnen) nahe, dieser konnte jedoch nicht gefunden werden. Nichtsdestotrotz zeigten sich die bewässerten Wiesen als ökologisch bedeutsames Habitat für Arthropodenarten feuchter Biotope. In einem kombinierten Labor- und Feldexperiment untersuchten wir die Veränderung der Nährstoffverfügbarkeit durch Bewässerung. Zwar ist heutzutage nicht mehr von einem direkten Düngeeffekt durch im Wasser geführte Schlacken auszugehen, aber dennoch zeigte sich ein indirekter Düngeeffekt der Bewässerung durch eine kurzzeitig stark erhöhte Pflanzenverfügbarkeit von Makro- und Mikronährstoffen. Die Ausprägung dieses Nährstoffpeaks und somit die Ausnutzung des sekundären Düngeeffekts zeigte eine graduelle Abhängigkeit auf Artebene, die eine spezifische Vegetationsentwicklung durch die Bewässerung untermauern. Diese Resultate legen daher nahe, dass Staubewässerung von Wiesen eine extensive Bewirtschaftungsform ist, die Biodiversität auf verschiedenen Skalenebenen fördert und gleichzeitig den Einsatz von Düngern reduzieren kann. Die Abstimmung von Düngung und Bewässerung bedarf jedoch der lokalspezifischen Evaluation abiotischer und biotischer Gegebenheiten.

CHAPTER 1

GENERAL INTRODUCTION

Isabell B. Müller

Grassland biodiversity & management

Biodiversity starts in the distant past and it points toward the future.
Frans Lanting, Saving Farmland (Nathalie Chambers), 2015

Grassland biodiversity in Europe

The existence of natural grassland in Europe began much earlier than the history of mankind. It is assumed that environmental conditions such as moisture deficits in steppe regions, low temperatures and short growing seasons above the timberline, natural floodplains as well as the grazing of megaherbivores throughout the Pleistocene maintained open grass-dominated habitats (Ellenberg & Leuschner 2010, Hejcman et al. 2013 and citations therein). During the Holocene, Central Europe persisted of a mosaic of forested and open steppe-like areas in the lowlands (Hejcman et al. 2013 and citations therein).

Semi-natural grasslands as we find them today in Central Europe had their origin when humans settled during the Neolithic. At this point humans began to control and modify the landscape to maintain and improve food supply to a larger extent. Neolithic livestock farming established the clearing of forested areas and constituted the origin of pastures (Ellenberg & Leuschner 2010). Until the Iron Age, livestock farming was the only management method to maintain grassland. Cutting of grassland and thus the establishment of hay meadows can only be dated back until the 7th-6th century BC (Heijcman 2013). The extensive grassland management led to highly diverse but fairly unproductive plant communities (Dierschke & Briemle 2008). Until the 18th century, the main purpose of hay production was to produce high quality forage for winter feeding. Since then livestock was increasingly kept in barns throughout the whole year to further produce farm yard manure (Hejcman et al. 2013 and citations therein), which lead to a large-scale expansion of hay meadows.

Today about 30 % of the agriculturally utilized area and 8% of the total land surface in Europe are covered by grassland (Isselstein et al. 2005). Central European grasslands belong to the most diverse habitats and are refugia for several rare and endangered species (Poschlod & WallisDeVries 2002, Duelli & Obrist 2003, Ellenberg & Leuschner 2010). Species-rich grasslands do not only harbor a high plant species richness, but also provide niches for many invertebrate and vertebrate species (Spehn et al. 2005) and are crucial for a variety of ecosystem processes as well as socioeconomic functions (Hopkins & Holz 2004). The high biodiversity in temperate grassland is a result of the interaction between regional heterogeneity in environmental conditions (soil parameters, geology, altitudinal and latitudinal gradients) but also extensive historical management regimes (Hopkins & Holz 2004). Patterns of land use have evolved over hundreds of years and formed a diverse mosaic of local habitats and species compositions (Jongman 2002, Poschlod and WallisDeVries 2002). With the ever-growing human population and the accompanied raising food demand during the High Middle Ages and even more during the Industrialization, economic requirements came to the fore (Strijker 2005). This led to a wide conversion of hay meadows to arable fields or intensively managed rangeland especially on profitable soils which used to harbor species-rich grassland communities. Livestock breeds with a high demand of high quality fodder made extensively managed permanent grassland unprofitable (Poschlod & WallisDeVries 2002). Abandonment of grassland management leads to succession into scrubland and forest since natural preservation of open habitats through wild-living large herbivores does not occur anymore as they became extinct all over Europe (Sutherland 2002, Pärtel et al. 2005). Furthermore, eutrophication through airborne nitrogen deposition as well as non-native species invasions pose a huge threat on grassland biodiversity (Stevens et al. 2004, Habel et al. 2013). From the establishment of managed grassland over a peak in species-diversity during the Middle Ages, grasslands in Central Europe are severely affected by management changes leading to species-diversity decline within the past 60 years. Consequently semi-natural, extensively managed grasslands belong to the most endangered habitats throughout Europe (Isselstein et al. 2005, Veen et al. 2009, Lepš 2014).

Grassland management intensification, abandonment of hay meadows and ongoing structural changes do not only have dramatic consequences for biodiversity, but also for ecosystem structures and ecosystem processes (Jongman 2002, WallisDeVries et al. 2002, Hector & Bagchi 2007, Riedener et al. 2013). Land use intensity is widely seen as the main cause of plant diversity as well as arthropod diversity loss in grassland ecosystems (Kleijn 2009, Allan 2014) which is most frequently ascribed to fertilization intensity (Socher et al. 2012, Simons et al. 2014). Human management practices going along with alterations of the species communities necessarily create chain reactions affecting other environmental and ecological levels (Fig.1; Chapin et al. 2000, Hooper et al. 2005). Species loss directly inhibits ecosystem resistance and resilience through the loss of functionally similar species as well as species interactions which act as a buffer for environmental changes and pests (Chapin et al. 2000). These changes control further biotic (faunistic and microbial community) and abiotic (soil properties) factors leading to a linkage of mutual impacts at several trophic levels (Chapin et al. 2000, Loreau 2000, Hooper et al. 2005). These effects do not only act on the local biodiversity (α-diversity) but also on the community at larger scales (β-diversity). β-turnover (biotic homogenization) through uniform management options threatens large-scale biodiversity more severely than direct loss of species as it causes multitrophic homogenization (Gossner et al. 2016).

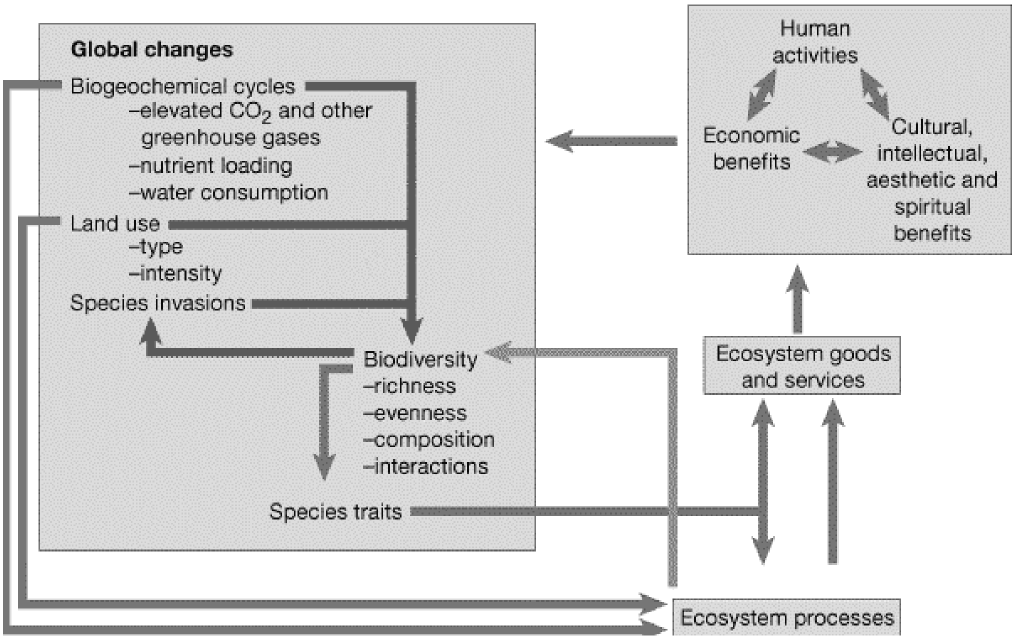

Fig.1. Feedback mechanisms of human management activities on several ecosystem properties. Human activities driven by socioeconomic motivations cause modifications at different ecological levels either directly or indirectly through adding further alterations in abiotic controls. This theoretical framework can be applied to all ecosystems worldwide (adapted from Hooper et al. 2005).

Locally adapted, extensive traditional grassland management options could be one way to foster heterogeneity at the landscape scale and protect regional multitrophic diversity which is endangered by uniformly applied and highly intensive forms of management (Kleijn et al. 2009, Gossner et al. 2016). Thus, promoting traditional extensive management to maintain regional biodiversity has become a prime goal of national and supranational environmental policy (Muller 2002, Isselstein et al. 2005). Agri-environment schemes encourage extensive grassland management by compensation payments, but their efficiency is under debate (Kleijn & Sutherland 2003, Kleijn et al. 2006, Knop et al. 2006). However, the maintenance or reactivation of traditional management options for conservation reasons is often costly and the outcome is uncertain. Thus, evaluations of traditional management options with respect to biodiversity and ecosystem functioning are urgently needed.

Nutrient availability - The crux for plant species coexistence

Growing economic demands on grassland led to an increasing use of mineral fertilizers to improve productivity. Fertilization and nutrient deposition is strongly linked to several ecological changes such as species community composition (species abundance, species richness and biomass production; Bobbink et al 2010, Phoenix et al. 2012, Basto et al. 2015) and biogeochemical cycling (Stehfest & Bouwman 2006).

Resource ratio models describe spatial heterogeneity of nutrient availability as the key mechanism for plant species coexistence (Tilman 1982, Tilman 1997). Plant species are able to take up nutrients at distinct spatial and temporal scales which results in niche differentiation allowing plant species to cope with heterogeneous nutrient availability and as follows coexist in diverse species communities (Harpole & Tilmann 2007). Nutrient enrichment through nitrogen and phosphorous fertilization diminishes the spatial heterogeneity of nutrient distribution and is therefore seen as the major factor directly influencing the plant species composition by changing the competitive structure within the plant community (Gough et al. 2000, Crawley et al. 2005, Harpole & Tilman 2007, Hautier et al. 2009, Lepš 2014). For decades studies assume a unimodal relationship between biodiversity and productivity, however, frequently this relationship proves to be weak depending on the specific plant species community as well as environmental gradients (Fargione et al. 2007, Fraser et al. 2015). The hump-shaped species diversity curve of Grime (1973) depicts the phenomenon that species richness (either flora or fauna) peaks at intermediate management intensity and drops rapidly if management and especially fertilizer input outreach a certain level of intensity. Studies taking Grime’s hump-shaped model into account explain that that moderate intensification with moderate nutrient input in low-fertility grassland promotes the growth of nitrophilous and mesophilous species, thus favoring species richness (Stehfest & Bouwman 2006). At high rates of fertilization, the positive effect of fertilization becomes capsized as productivity increases and light becomes the most limiting factor, allowing only a few faster-growing and taller species to compete successfully (Tilman 1982, Suding et al. 2005, Hautier et al. 2009). Negative effects of fertilization on plant species communities can affect other trophic levels as well: Increased biomass production and changes in the physical structure of the sward impact arthropod diversity (Morris 2000, Woodcock et al. 2005, Woodcock & Pywell 2009) as the diversity of invertebrate trophic levels relies on a complex vertical and horizontal vegetation structure (Woodcock & Pywell 2009, Dittrich & Helden 2011). However the relationship between the physical sward structure and arthropod diversity seems scale-dependent and varies highly across species communities (Waide et al 1999, Gough et al. 2000).

Not only are the agriculturally used ecosystems affected by high rates of fertilization as the amount of fertilizer applied often surpasses the plant's nutrient utilization efficiency. The insufficient nutrient utilization necessarily leads to hydrological leaching or volatization of nutrients into non-target ecosystems (Röckström et al. 2009). Eutrophication due to nutrient input and deposition is seen as one of the major global drivers of biodiversity loss (Röckström et al. 2009). This is essentially a problem for N fertilization since N is the mostly limiting factor in terrestrial ecosystems (Vitousek et al. 2002) and so high doses of N fertilizers are applied worldwide. Overdosing of N fertilizer leads to hydrological leaching of NO_3 as well as gaseous emissions of NH_3, NO, N_2O (Bouwman et al. 2002, Galloway et al. 2003). The offset of reactive N and atmospheric deposition into non-target ecosystems is a global problem as it affects both biodiversity and ecosystem functioning. Worldwide the human conversion of N_2 into reactive forms exceeds the natural terrestrial N_2 conversion by a factor of three (Rockström et al. 2009, Fowler et al 2013, Vitousek et al 2013). Thus the planetary boundary for the N cycle has already been surpassed (Rockström et al. 2009, Steffen et al. 2011). Nevertheless it is still inevitable to further dam the pollution of non-target ecosystems. This makes it necessary to define targeted management options which serve to maintain or even improve stand productivity and allow a reduction of fertilizer costs at the same time.

Meadow irrigation

History and future development

Irrigation of agroecosystems to increase productivity is historically old and still widespread on a modern basis in crop production systems. However, artificial flooding of meadows used to be a common irrigation management strategy for centuries all over Europe but has become nearly forgotten today. Before the invention of industrially produced fertilizers it was one of the most efficient methods to compensate the loss of nutrients after mowing and to increase the yield (Hassler 1995). It is assumed that the solutes and particulate matter of the rivers were transported into the meadows through irrigation and caused a fertilization effect. Thus water with high loads of fine suspended material such as glacier melt water as well as water from loess areas seemed to be very effective for fertilizing irrigation (Leibundgut & Kohn 2014a). Moreover streams carried untreated wastewater which can be expected to be the major reason for the fertilization effect (Hassler 1995) but also the discharge of manure from adjacent agroecosystems. In lowland regions the irrigation water was commonly even enriched with manure in pits and ponds before applied onto the meadows (Hassler 1995). A positive side effect of irrigation is soil temperature regulation and soil warming in spring which may cause an earlier onset of the vegetative period as well as protection from extreme heats during summer (Cutting & Cummings 2007, Cook et al 2015).

Due to the structural heterogeneity of landscapes, there are various techniques of meadow irrigation. In lowland areas, the characteristic technique used to be flood irrigation. The water of the nearby river was dammed and led into the meadows through a system of ditches. In mountainous regions, slope irrigation with a system of contour parallel ditches has been developed. Predominantly in England, ridge structures were built with the irrigation ditch on top of the ridge to descend the irrigation water through the slope (bedwork system; Cook 2010). In bedwork meadows in England *Holcus lanatus* and *Agrostis stolonifera* were found to be the dominant species and were thus described to be typical for water meadow plant communities (Cummings 2007). A dominance of grass species was also proofed in dry weight biomass of the same meadows in England with irrigated sites displaying a higher proportion of monocotyledones than the unfloated controls (Cook et al. 2004). This gives evidence to higher yields from irrigated meadows which was handed down through history but also found in observational studies (Cook et al. 2004, Stearne & Cook 2007).

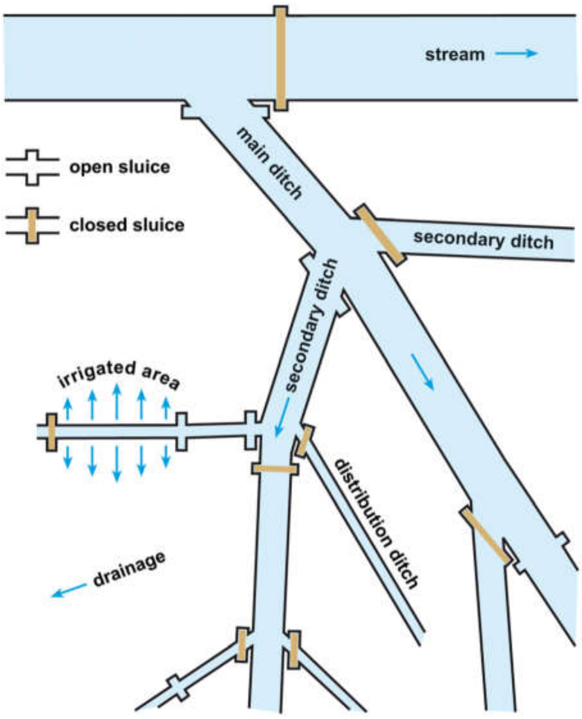

Fig. 2. Scheme of the lowland meadow irrigation system (adapted from Leibundgut & Kohn 2014a).

Just like the decline of semi-natural hay meadows, the abandonment of traditional irrigation systems came along with the wide societal and economic changes during the 20th century (Leibundgut & Kohn 2014a). The quest for higher productivity and the emergence of synthetic fertilizers opened the way for agricultural management intensification and made the labor-intensive traditional irrigation systems widely unprofitable (Strijker 2005, Baur et al 2006, Stearne & Cook 2007). Today these traditional grassland irrigation systems are either replaced by sprinkler-irrigation or completely abandoned (Riedener et al. 2013). In Germany, meadow irrigation decreased from about 250.000 ha to a few thousand hectares throughout the 20th century (Leibundgut 2004). Today traditional water meadows with active flood irrigation have remained only in a few regions, being supported by nature conservationist approaches. Most recently, traditionally irrigated grasslands are increasingly encouraged in the scope of biodiversity conservation as these so-called water meadows have been recognized as refugia for many protected plant, amphibian, grasshopper and Ondonate species (Leibundgut & Kohn 2014b and citations therein) but also as important sites for breeding birds (Cook & Williamson 1999, Cook 2010, Leibundgut & Kohn 2014b).

There is only few data available about the plant species composition in artificially flooded meadows. In contrast to fertilization we can assume that a moderate watering with a low nutrient input has a minor impact on the species communities since the nutrient input can be expected to be low and many drought indicator species are still able to cope with short-term moist conditions (Hassler 1995). Available data on the species communities and yield show high regional variation so that it has to be assumed that long-term irrigation practice acts site-specific as a matter of abiotic but also biotic factors (Cummings 2007). Cycles of flooding and draining cause characteristic vegetation patterns that display the alternating soil moisture conditions (Hoppe 2001). Although technical installations aim to apply the irrigation water homogeneously, traditional forms of irrigation such as flood irrigation foster the establishment of microscale islands of different water and resource availability due to the microrelief of the meadows. This microscale heterogeneity may result in a higher floristic and faunistic diversity (alpha diversity) in traditionally irrigated meadows (Rosenzweig 2004). Moreover, the irrigation ditches themselves provide habitats for a high number of species (Leibundgut & Kohn 2014b). Further, the regionally distinct technical installations of irrigation systems can be expected to foster heterogeneity at the landscape level and thus beta diversity. Thus, traditional irrigation systems offer a great potential for biodiversity conservation at the regional as well as at the landscape scale.

Today, rivers do not carry as heavy loads of sewage anymore since wastewater becomes filtrated. Nevertheless, nutrient availability is strongly bound to abiotic factors especially water availability. Longer drought periods during the summer will necessarily inhibit plant nutrient uptake during these times. Irrigation is a way to bridge water deficits during the drier periods and to sustain plant productivity by maintaining nutrient supply. The short-term water pulses as created by irrigation promote plant nutrient uptake (Leonardson et al. 1994) and are thus likely to increase primary productivity. The increased nutrient use efficiency in irrigated meadows may result from an enhanced mineralization rate and the mobilization of exchangeable nutrients (Leonardson et al. 1994, Austin et al. 2004) such as biologically available phosphorous and nitrogen (Cook et al. 2003). Just like the historical practice of liquid manure application with the irrigation water, a coupling of irrigation and fertilizer application could be a sustainable way to improve nutrient use efficiency and consequently reduce fertilization intensity without deficiencies in productivity.

Facing the predicted climate shifts in Central Europe as well as the threads of mineral fertilizers on the biodiversity of grassland, irrigation may represent a bridge between agricultural needs and the conservation value of grassland biodiversity. From today’s perspective, traditional irrigation practices are extensive and could thus be described as a sustainable management practice to balance biodiversity protection and maintain agronomic necessities at the same time (Leibundgut and Kohn 2014a). Nevertheless, there is and will always be a trade-off between the maintenance or increase of productivity on the one hand and the protection of biodiversity on the other hand. This makes it necessary to define target-oriented management options which are suitable to regional specifications and the requirements of the local species communities. The value of the preservation and further development of traditional land use strategies such as meadow irrigation has thus to be estimated based on their sustainability, economic necessities and environmental capacities (Vos 1999, von Haaren 2002).

Objectives of the dissertation thesis

This study was conducted within the framework of the AufLand Research Initiative. AufLand is an interdisciplinary project which aims to investigate the interactions at the land-water interface. The subproject “Wässerwiesen” uses traditionally flood irrigated meadows near Landau (Germany) to investigate the reciprocal impact of grassland irrigation and fertilization on the biodiversity, biomass production and ecosystem processes, particularly nutrient allocation and turnover.

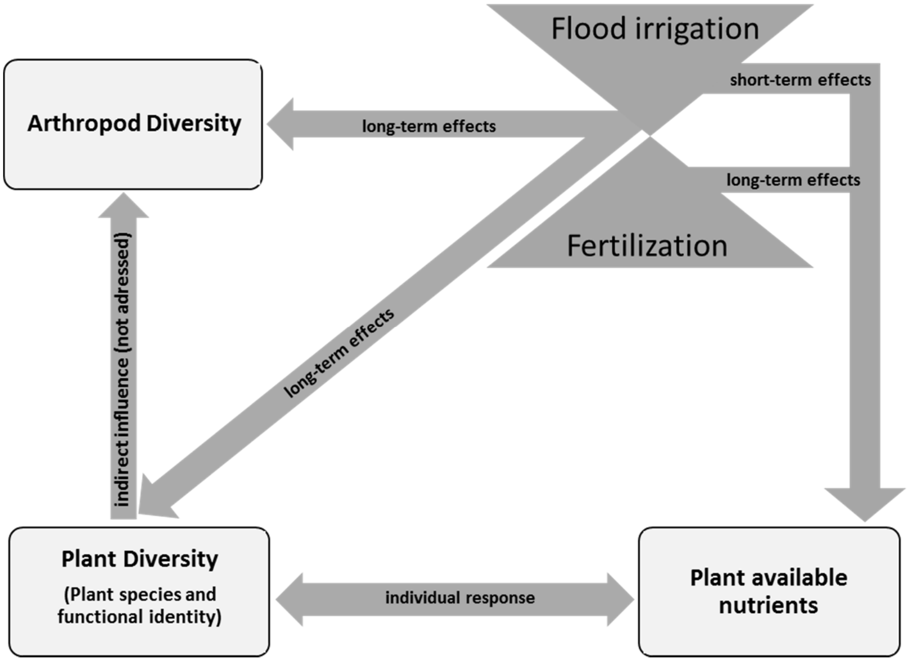

Fig.3. Theoretical framework of the thesis objectives.

The thesis is subdivided into two studies combining field studies as well as controlled laboratory experiments focusing on the interplay between plant diversity and nutrient cycling under traditional flood irrigation.

I. First, in a field study, vegetation (species and biomass) and invertebrate samplings were conducted to directly compare irrigated and non-irrigated meadows with and without fertilization over a two year period.
   The vegetation study hypothesized flood irrigation to foster plant and invertebrate diversity at different scales (species and functional group composition).
II. The second study combined a field study with the experimental study of nutrient availability and nitrogen utilization efficiency under traditional flood irrigation. The field study aimed to analyze the impact of management (irrigation and fertilization)

on the rhizosphere nutrient availability and the plant's nitrogen utilization efficiency. The experimental approach aimed to investigate the plant species effect on rhizosphere nutrient availability and nitrogen utilization efficiency under flood irrigation. Flood irrigation was assumed to increase plant nutrient availability and nitrogen utilization efficiency. This effect was expected to be more or less pronounced depending on plant species cover as well as the specific management regime.

The evaluation of the plant functional composition (Chapter 2) allows to draw conclusions on ecosystem processes which on the one hand have influenced the establishment of the specific plant functional community but are on the other hand modified by the specific plant functional community. Shifts in the plant functional community are reflected in the plant diversity (Chapter 3) of the meadows which was studied on the site (α-diversity) as well as on the landscape scale (β-diversity). Changing wet-dry cycles as caused by irrigation as well as the establishment of specific plant communities are likely to directly shape the arthropod community (Chapter 4) and thus impact the diversity of the fauna within the meadows. Biodiversity measures give rise to the conservation value of the meadows as our results reflect the long-term impact of traditional flood irrigation on the plant and arthropod community. The immediate effect of irrigation on the plant available nutrients as well as the nitrogen use efficiency was expected to be a measure of the species-specific rhizosphere which is closely related to plant functional attributes (Chapter 5). In conclusion, our results form the basis for the evaluation of traditional flood irrigation as a potentially sustainable management option for grassland which combines both conservation benefits as well as the maintenance of agronomic demands.

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CHAPTER 2

PLANT FUNCTIONAL SHIFTS IN CENTRAL EUROPEAN GRASSLAND UNDER TRADITIONAL FLOOD IRRIGATION

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Abstract

Questions: Lowland meadow irrigation used to be a widespread management practice to improve hay yield in Central European grasslands. Recently, traditional meadow irrigation is being re-established in some parts of Europe. Nevertheless, the consequences of the regular artificial flooding on the vegetation of these water meadows remain poorly understood. We studied the impact of flood irrigation on the plant functional and species composition of extensively managed hay meadows.

Location: Lowland of the river Queich between Landau and Lustadt (DE, Rhineland-Palatinate; 49° 11′ 52.9″ N, 8° 7′ 34.2″ O).

Methods: We sampled vegetation in 34 meadows which differed in irrigation status (irrigated/non-irrigated) and fertilization (unfertilized/fertilized). Plants were classified into functional groups according to growth forms, N-fixing ability and reproductive strategy. Effects of meadow irrigation on the plant functional composition were analyzed using two complementary approaches. In the “community approach”, we analyzed total cover of each functional group per meadow with respect to irrigation and fertilization. In the “species approach”, we analyzed the mean response to irrigation among the species within the defined functional groups.

Results: Total cover of rosettes and semi-rosettes increased relative to graminoids in irrigated meadows. Cover of legumes was three times higher in irrigated compared to non-irrigated meadows. Irrigation enhanced preferences for seed and vegetative reproduction. However, the response of the individual species within the functional groups was inconsistent. Fertilization had an overall minor influence on the functional composition of the meadows.

Conclusions: The higher proportion of plants with basal growth organs in irrigated meadows surrogates that irrigation may enhance a more complex vertical structure of the vegetation. Enhancement of rosettes, semi-rosettes and legumes at the cost of graminoids by irrigation was more significant in the community than in the species approach, indicating that the functional group response was amplified by the respective dominant species. This highlights the importance to consider species-level interactions in functional vegetation analysis.

Introduction

Until the 20th century, agricultural production was strongly limited by local site conditions and resource availability. This led to a high regional heterogeneity and specific species composition in grassland ecosystems, making them an integral part of the semi-natural landscape of Central Europe (WallisDeVries et al. 2002, Duelli & Obrist 2003). Agricultural intensification since the mid-20th century has led to increasing structural and biological homogenization or even loss of grasslands (Jongman 2002, Isselstein et al. 2005, Maurer et al. 2006). In intensively managed grasslands, few productive forage grasses outcompete other plant species and functional groups (such as tall herbs and legumes), which substantially affects ecosystem structure and functioning (Isselstein et al. 2005, Martin & Sauerborn 2013).

Grassland management affects the taxonomic and functional plant composition through multiple combinations of resource availability and disturbances (Quétier et al. 2007). The most influential factors are regular defoliation and modification of nutrient availability through fertilization but also site-specific traditional extensive management regimes. Traditional meadow irrigation is one of these extensive management options. Over large parts of temperate Europe and the Mediterranean regions, traditional meadow irrigation used to be a common way for soil improvement and pest control before the introduction of chemical fertilizers and pesticides (Leibundgut 2004, Schellberg 2005). During the 20th century, meadow irrigation was widely abandoned and decreased from about 250 000 ha to a few thousand hectares solely in Germany (Leibundgut 2004). Adapted to the topography of the landscape, there are several different irrigation techniques. In lowland areas, the water of nearby rivers is used and distributed either by the natural gradient of the meadow (Schellberg 2005) or, like in our study area, dammed by weirs and led into the meadows and back into the river through a system of main and drain ditches. More recently these historical irrigation systems were rediscovered for nature conservation and agri-environment schemes. In some regions historical water meadows are being re-established but the long-term consequences of this management system remain poorly understood. Recent studies in irrigated meadows in montane areas as well as lowland areas revealed considerable effects of irrigation on the species assemblages of vascular plants and invertebrates (Riedener et al. 2013, Andrey et al. 2014, Schirmel et al. 2014).

Functional vegetation analysis can reveal the impact of environmental changes on ecosystem properties and functions (Grime 2001, Louault et al. 2005, Quetiér et al. 2007). We expect that irrigation and fertilization induced plant functional shifts, since both water and nutrient availability are driving vegetation shifts by altering the competitive structure in the plant community (Dierschke & Briemle 2002). Light interception is a major factor for the competitive structure within grassland plant communities (Hautier 2009). Traditional flood irrigation is often heterogeneous and the patchy water and sediment distribution result in small-scale differences in soil water conditions. Irrigation can modify the micro-relief and create small-open patches which may increase light availability at the ground (Hoppe 2001). Moreover, irrigation alters nitrogen availability by enhancing microbial mineralization processes and plant nitrogen uptake (Leonardson et al. 1994). In contrast, fertilization strengthens light competition (Hautier et al. 2009) and can alter mineralization processes because additional nitrogen availability stimulates microbial activity (Blume et al. 2010).

Here we studied the effects of irrigation and fertilization on plant functional groups (growth form, nitrogen-fixing ability and reproductive strategy) which cover the major aspects of plant functionality and vegetation structure demonstrating establishment success and persistence. Especially in fertilized grasslands, subordinate species such as rosettes and semi-rosettes are outcompeted by tall graminoids due to light competition (Hautier et al. 2009). Nitrogen-fixing species (legumes) have an outstanding ecological relevance for nitrogen cycling but their abundance is influenced by nutrient availability. In general, they are favored in nitrogen-limited ecosystems through their ability to fix atmospheric nitrogen symbiotically. Traits dealing with plant reproductive strategies such as vegetative reproduction by lateral spread or sexual reproduction by seed dispersal, respectively, reflect both resource availability and disturbance level. Seedlings are highly sensitive towards periods of drought and water stress (Fenner 1987). Irrigation could thus enhance seedling survival and increase establishment success of seeding species either directly through enhanced water availability or indirectly due to the improved nutrient availability (Davis et al. 1999, Dickson & Foster 2008). Vegetatively reproducing species, such as clonal grasses and herbs, are capable of exploiting heterogeneous nutrient distribution more efficiently than other groups and thus benefit from intensive fertilization (Eilts et al. 2011).

We studied effects of flood irrigation and fertilization on vegetation in hay meadows along the river Queich, Germany, in a two-factorial design. We expected effects on the plant species and functional composition and hypothesized (Ia) plants with basal growth organs (rosettes and semi-rosettes) to be favored by irrigation through increased light availability, whereas fertilization is expected to have opposite effects. (Ib) Graminoids are promoted mainly by fertilization and are less successful in irrigated unfertilized meadows. (Ic) Legumes are expected to benefit from irrigation through nitrogen loss with the irrigation water (leaching) and thus have growth advantages especially in irrigated unfertilized meadows. (Id) Plant species with sexual reproduction will profit from irrigation through improved water conditions during summer and the increased light availability, whereas fertilization is expected to have opposite effects. Finally, we expected (II) similar responses of the species within one functional group towards irrigation and fertilization.

Methods

Study Area

The study was carried out in 34 meadows in the lowland of the river Queich between Landau and Lustadt (DE, Rhineland-Palatinate; 49° 11′ 52.9″ N, 8° 7′ 34.2″ O, Fig.1). The annual mean temperature of the region is 10.5°C with an annual precipitation of 667 mm (station Landau; German Weather Service). Soils of the alluvial sediments are sandy to loamy (Briem & Geiger 2008). The study area is located in the NATURA 2000 area “Bellheimer Wald und Queichtal”. This area covers about 4,500 ha of which 70% are forests and the remaining 30% are mainly grasslands. The irrigation history in this region can be traced back until the mid-15th century (Fiedler 1965). Irrigation was mainly abandoned in the 1950s-1970s and partly reactivated for nature conservation within the last 15 years. However, some of the meadows have been continuously irrigated since the 17th century. These historical changes in meadow management strategies have created a mosaic of irrigated and formerly irrigated meadows, which furthermore show a range of management intensities. The studied meadows are lowland hay meadows (mesophilic grasslands) belonging to the Arrhenatherion eliatoris alliance. Codominant species are *Alopecurus pratensis, Galium album* and *Sanguisorba officinalis* (Keller 2013).

The meadows were selected according to irrigation status (N irrigated meadows = 20; N non-irrigated = 14) and fertilization (N unfertilized = 17; N fertilized = 17). Irrigated meadows received water three to four times per year (spring, summer) for at least the past five years. Non-irrigated meadows have not been irrigated for at least 50 years. The traditional flooding method in the region is to dam the water of the river and let it stream into the meadows and back into the river through a system of open water channels (lowland irrigation type; Leibundgut 2004). This leads to a relatively homogeneous water flow to prevent stagnant moisture (Hassler 1995). Each flooding event lasted two to three days. Fertilized meadows received 6.5 - 70 kg N/ha^{-1} applied as NPK or CAN fertilizer. The amount of applied nitrogen was calculated from the amount of fertilizer used. All meadows underlay similar extensive rotational winter grazing by sheep with yearly changing stocking rates and were usually mown two times annually in June and August/September. Data regarding irrigation status, amount and type of applied fertilizer, grazing and mowing intensity was obtained by personal interviews with the landowners and farmers.

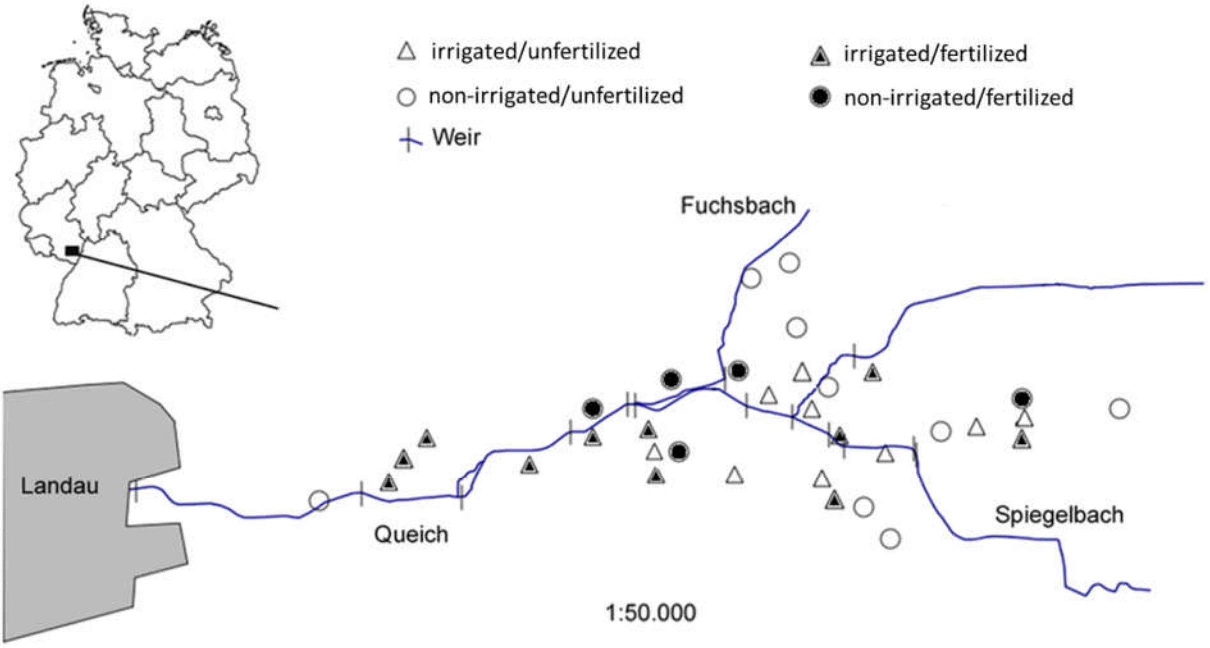

Fig.1. Location of the study sites in the Queich lowland (adapted from Schirmel et al. 2014).

Vegetation survey

On each meadow we randomly installed one 50 x 50 m plot (n = 34 plots) using ArcGIS (version 9.3, Environmental Systems Research Institute, Inc., CA, US). Plots were installed keeping a buffer zone of at least 10 m to adjacent habitats or elements (e.g. ditches, trees, forest) to avoid edge-effects. Neither irrigation nor fertilization was spatially autocorrelated, which was tested prior to the analyses with Moran's I correlograms (Legendre & Legendre 1998; Appendix S2) using SAM (version 4.0, Rangel et al. 2010).

On each plot we randomly located three subplots of 3 x 3 m (n = 102). In each subplot vegetation was sampled twice in 2012 (May and August). Species projection cover (%) was estimated using a percentage scale estimation table (1-100%). Species with only one individual per subplot were marked as 0.1. Plant species were identified according to Wisskirchen & Haeupler (1998).

Functional groups were defined according to ecologically relevant attributes describing spatially complementary resource use and vertical vegetation stratification. To account for the vertical structure of herbaceous species communities, we used leaf distribution along the stem (growth form) to subdivide the species into rosettes, semi-rosettes and species with only stem leaves (further referred to as non-rosettes). All species of the Poaceae, Cyperaceae and

Juncaceae were assigned to the graminoid group due to their common perennial life cycle and caespitose growth. Data on the leaf distribution along the stem was obtained using CLO-PLA (database of clonal growth in plants; Klimešová & Klimeš 2006; http://clopla.butbn.cas.cz) and LEDA traitbase (Kleyer et al. 2008; http://www.leda-traitbase.org). If one of the databases offered more than one entry the most frequent was chosen. Further we analyzed the abundance of nitrogen-fixing species by subdividing all species except graminoids into N-fixing (legumes) and non-N-fixing herbs. Legumes were all species belonging to the family Fabaceae (genus *Lathyrus, Medicago, Trifolium, Vicia*). Furthermore, we analyzed reproductive strategy as the degrees of preferences for sexual (s) respectively vegetative (v) reproduction of each species. Data on the reproductive strategy was taken from the Biolflor traitbase (Klotz et al. 2002). The reproduction types were not calculated as mean cover since there are various intermediate reproduction types (sv, ssv, vvs). We followed Burmeier et al. (2010) who divided all types into their single components using a point system. Species receive points according to the proportion of the strategy. Thus, sv reproduction types receive one point for each strategy (1.5/1.5) whereas exclusively s reproduction types would receive 3/0 and mainly vegetatively reproducing species (vvs) received 2/1. Based on this, we calculated weighted proportions of the reproduction types for each subplot.

Data Analysis

We combined spring and summer data for all statistical analyses by averaging percent cover values for each subplot. Cover values of the three subplots per plot were averaged and analyses were carried out with the 34 plots. Statistical analyses were performed with R (version 2.15.1, R Core Team 2014, R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/) using the packages vegan (Oksanen et al. 2011) and MASS (Venables & Ripley 2002).

Effects of irrigation and fertilization on functional groups were analyzed in two contrasting ways (Entling et al. 2010). First, we used the overall cover of each functional group (sum of all species) as dependent variable. Since our data were non-normally distributed we applied quasi-Poisson generalized linear models (GLM; R command ‘glm’) to determine the effects of irrigation and fertilization on the functional groups (Warton 2011). For growth form and N-fixing ability we tested how their mean cover was affected by irrigation and fertilization. Effects of irrigation and fertilization on the reproduction types were also analyzed using GLM’s. Since the interaction between irrigation and fertilization was not significant in any of the models we backward removed the interaction term and report only the main effects.

However this “community approach” bears the risk that the overall cover of a functional group is determined by one or few dominant species. Hence, the response of dominant species may be wrongly interpreted as a shift in traits even if the majority of species from the same functional group respond in the opposite direction. To overcome this problem, we characterized the response of each species to irrigation (species as replicates). In this “species approach”, we calculated species “affinity” towards irrigation expressed as Spearman rho. Then we applied linear models (lm; R command ‘lm’) to test whether the mean irrigation affinity of all species within a functional group differs significantly from zero (i.e. if species from a functional group prefer or avoid irrigated meadows on average). By means of nonmetric multidimensional scaling (NMDS, command ‘metaMDS’ in the R package ‘vegan’) we displayed the plant species composition and the related environmental parameters (Leyer & Wesche 2008). We used Bray-Curtis dissimilarity and a maximum of 100 random starts. Correlations of environmental variables (irrigation [yes/no], fertilization [yes/no] and amount of nitrogen) with vegetation composition were tested with 1000 permutations.

Results

Functional composition: Community approach

As hypothesized, irrigation influenced plant functional composition while, on the contrary, fertilization had no significant effects (Fig 2a, Tab.1). Irrigation significantly increased the cover of rosettes and semi-rosettes but non-rosettes remained unaffected. Graminoid cover was significantly higher in non-irrigated than in irrigated meadows. We found a significantly higher cover of legumes in irrigated meadows while non-N-fixing plants were not affected by irrigation. Irrigation favored both sexual and vegetative reproduction preference.

Table 1. Effects of irrigation (yes/no) and fertilization (yes/no) on functional group cover (growth form, N-fixing ability, reproduction type (weighed means). Results are based on quasi-Poisson GLM´s (n=34). (*) = p<0.1; * = p<0.05; ** = p<0.01; *** = p<0.001.

		Irrigation			**Fertilization**		
Functional group	**Residual df**	**t-value**	**Standard Error**	**p**	**t-value**	**Standard Error**	**p**
			Growth form				
Rosettes	31	2.87	2.771	0.007**	-0.97	2.727	0.338
Semi-rosettes	31	3.36	7.019	0.002**	-1.01		0.340
Non-rosettes	31	-0.95	5.432	0.347	-0.86	5.347	0.393
Graminoids	31	-2.46	6.064	0.018*	0.87	5.969	0.380
			N-fixing ability				
Legumes	31	3.89	3.907	0.0006***	-1.11	3.846	0.306
Non-N-fixing	31	1.49	7.271	0.144	-1.39	7.156	0.174
			Reproduction type				
Seeding preference	31	3.28	0.047	0.002**	0.54	0.047	0.590
Vegetative preference	31	3.25	0.065	0.002**	0.31	0.064	0.752

Functional composition: Species approach

The species approach revealed a significant effect of irrigation only for legumes, i.e. species reactions within all other functional groups were non-uniform. Legumes were marginally positively related to irrigation (t = 2.19, p = 0.052; Fig.2b). The most abundant within a total of ten legume species was *Trifolium pratense*, which had the highest cover in irrigated meadows (t = 3.94, p = <0.001; Appendix S1). In contrast to the community approach, effects of irrigation were non-significant for rosette (t = 0.94, p = 0.38), semi-rosette (t = 0.83, p = 0.41), and graminoid (t = -0.86, p = 0.39) species. However, for rosettes only two (*Leontodon hispidus* and *Allium vineale*) out of 7 species responded in the opposite direction of the remaining species. In the semi-rosettes group 17 out of 32 species responded positively to irrigation. For the graminoids we found 15 out of 25 species with a positive response to irrigation.

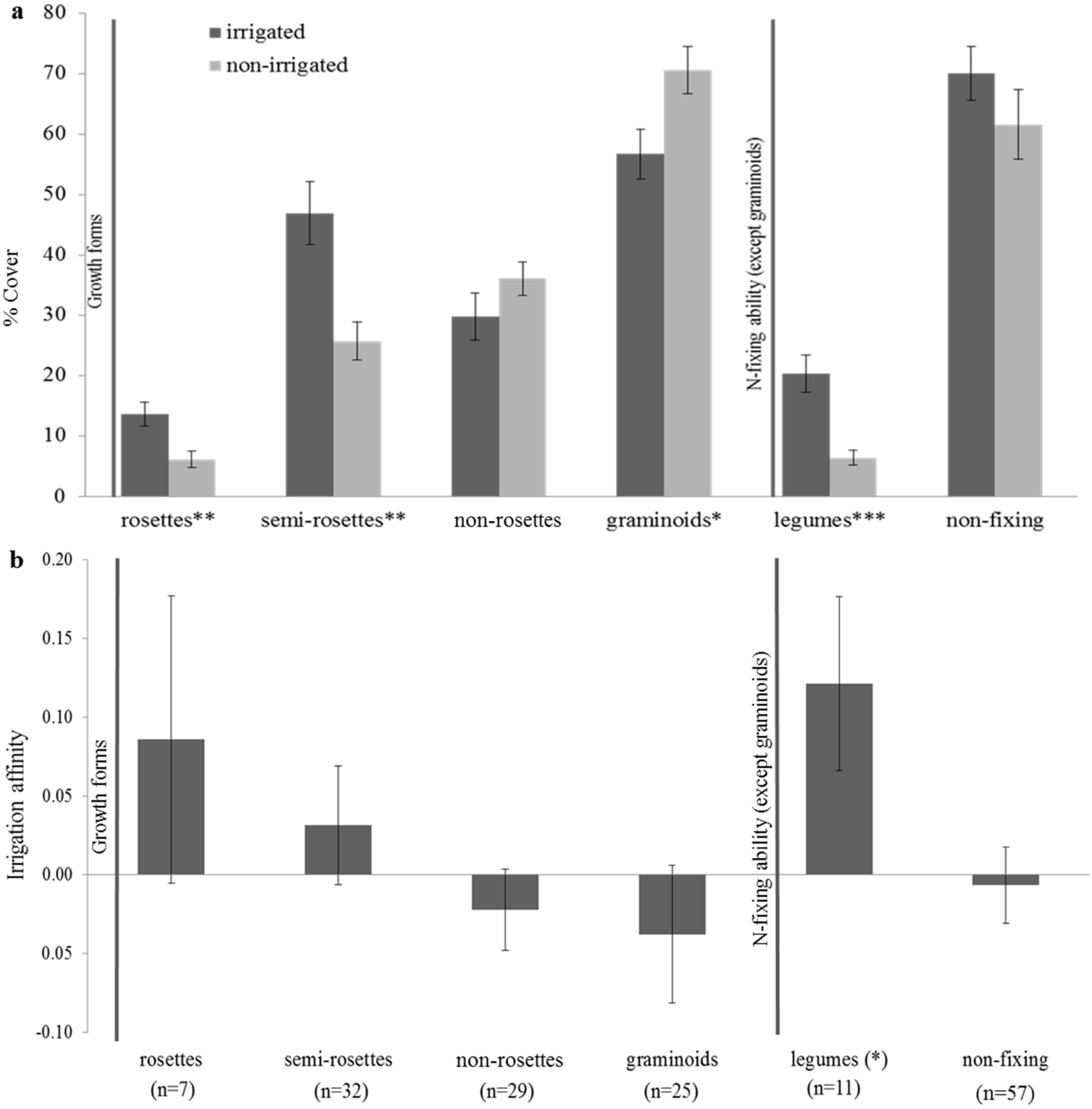

Fig. 2. Functional group shifts induced by meadow irrigation according to the community and the species approach. The a) community approach is based on differences of the mean cover of the studied functional groups (growth form, N-fixing-ability) on plot level (n = 34), the b) species approach is based on the mean preference of species within functional groups for irrigated meadows (Spearman rank correlations). Positive coefficients indicate higher abundance of species under irrigation. (*) $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Error bars = ± standard deviation.

Species composition

Species composition in irrigated versus non-irrigated meadows was grouped with little overlap (3 dimensions, stress = 0.16; Fig. 3). Irrigation (n = 34, r^2=0.43, p=0.001) and fertilization (n = 34, r^2=0.24, p=0.02) significantly affected community composition. Moreover, species composition correlated significantly with the amount of applied nitrogen (r^2=0.24, p=0.01).

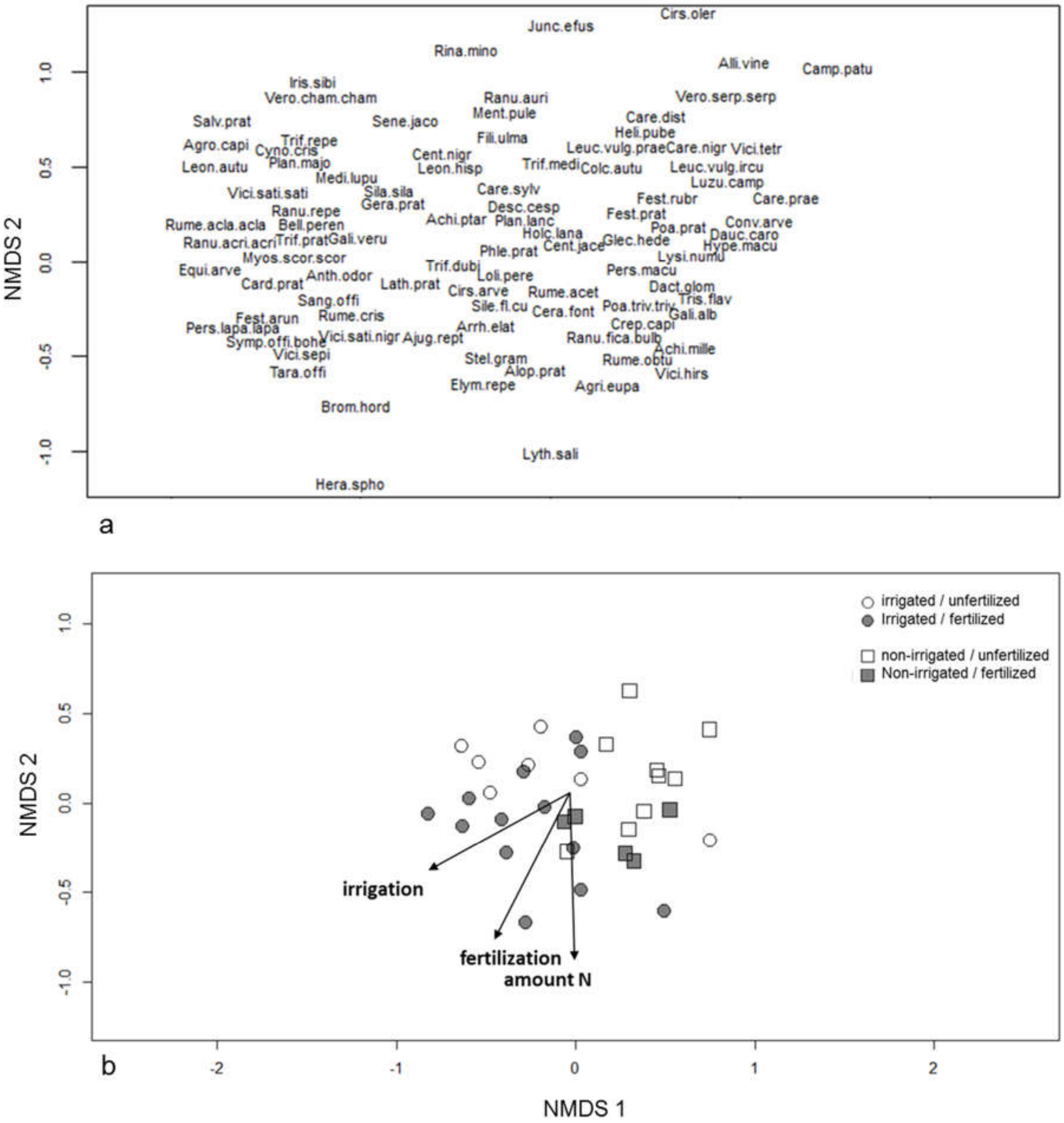

Fig.3. Dissimilarity of irrigated and non-irrigated meadows based on their vegetation composition. NMDS ordination plot of the (a) species distribution, (b) sites (n=34) and fitted environmental variables. Categorical variables irrigation (yes/no) and fertilization (yes/no) were numerically coded (100/0). Species abundances in irrigated and non-irrigated sites are found in Appendix S1.

Discussion

As hypothesized, we found strong effects of irrigation on plant species composition and functional groups (growth forms, N-fixing ability, reproductive types). However, species within functional groups showed contrasting reactions towards irrigation except for legumes, which were favored by irrigation. Surprisingly, fertilization had no significant influence except on species composition. The dominant effects of irrigation on plant functional and species composition do not go along with the response of plant diversity: Plant species richness was unaffected by irrigation, but negatively influenced by fertilization (Rudolph et al., data not shown). Apparently irrigation shapes plant species communities without affecting the number of species occurring at the site which may underlie the individual responses of species towards irrigation as found in the species approach.

Functional composition

In accordance with hypothesis Ia, rosettes and semi-rosette plants benefitted from irrigation. This is in accordance to Riedener et al (2013), who found increasing proportions of rosettes and semi-rosettes with irrigation intensity. Species with basal growth organs, such as rosettes and semi-rosettes, compete primarily for light. Although technical installation of the water channels aims to ensure a relatively homogeneous water flow, the ground is inundated irregularly depending on the micro-relief (Meurer & Müller 1987). This may lead to small-scale open patches which can be occupied by light-demanding rosette and semi-rosette species. The increased coverage of plants with basal growth organs did not coincide with overall increased species richness in irrigated meadows, which is surprising given that light availability at ground level can limit plant diversity (Hautier et al. 2009). Thus, and because of the non-significant response of rosettes and semi-rosettes in the species approach, we cannot exclude that their positive response to irrigation reflects specific preference of the dominant species rather than a general response of the functional group. Nevertheless within the rosettes and semi-rosettes group the most common species were positively correlated with irrigation. Within the semi-rosettes the hygrophilic species *Ranunculus repens* and *Sanguisorba officinalis* had the highest correlation coefficient with irrigation indicating potentially positive influence of irrigation on the formation of hygrophilic species communities which may be promoted with more frequent and longer irrigation events.

As expected (hypothesis Ib), we found a reduced graminoid cover in irrigated meadows. A lower grass/forb ratio (forb = all herbs except legumes) in traditionally flood irrigated hay meadows in Switzerland has also been shown by Riedener et al. (2013) and Andrey et al. (2014). This finding can be explained again by the formation of small scale open patches which favor the establishment success of subordinate species (e.g. species with basal growth, see above) and result in an overall lower dominance of graminoids (i.e. a mean of 56.6% in irrigated vs. 70.5% in non-irrigated meadows). Since many dominant graminoid species are rhizomateous clonal species and thus able to exploit heterogeneous nutrient distribution by lateral spread and nitrogen transfer between clones, we expected them to be favored in fertilized meadows (Honsová 2007, Eilts et al. 2011). However, our data could not prove any effect of fertilization on graminoid cover as hypothesized. Apparently the meadow management in the Queich lowland is half-extensive to half-intensive (Dierschke & Briemle 2008) with relatively low nitrogen fertilization, which would explain the overall minor influence of fertilization on the plant functional composition in our study area.

Irrigation had a positive effect on legumes, which confirms our hypothesis Ic. The increased proportion of legumes in irrigated meadows can be expected to be relevant for nitrogen cycling and consequently nitrogen availability for non-N-fixing species (Gubsch et al. 2011). Even stronger than in our study, shortgrass prairies showed a 30 times increase of legume density under irrigation treatment (Lauenroth & Dodd 1979). Other studies found enhanced nodule formation and functioning in legumes under increased soil water availability (Vincent 1965, Zahran 1999). Andrey et al. (2014) found similar positive effects on legume cover in sprinkler-irrigated meadows of the inner Alps in Switzerland. Thus, it seems that legumes benefit from irrigation irrespective of the specific technique. The positive effect could be a result of enhanced fixation activity through the additional water supply during the dry seasons. However, higher density of legumes was governed mainly by the most abundant species *Trifolium pratense.* Nitrogen-fixation varies strongly between legume species, which can explain the more variable results in the species compared to the community approach. *T. pratense* is an effective nitrogen fixing species (Blume et al. 2010) and would thus benefit from competitive advantages through nitrogen fixation in irrigated meadows. The semi-rosette growth from of *T. pratense* provides an additional explanation for its high cover in irrigated meadows. The competitive ability of legumes is normally reduced by mineral nitrogen fertilization (Lauenroth & Dodd 1979). In contrast to the response towards irrigation, our results unexpectedly did not show any significant effect of fertilization on legumes density.

As hypothesized (Id), irrigation significantly enhanced the preference for seed reproduction. In general, low soil water contents reduce seed germination rate (Evans & Etherington 1990). Irrigation during the dry summer months could reduce the desiccation of seedlings, which would explain their reproductive success in irrigated meadows. Another factor for the success of seeders in irrigated meadows could be seed dispersal with the irrigation water (Poschlod & Bonn 1998). Dispersal is an important limiting factor for the distribution of plants both on the local and continental scale (Poschlod et al. 2013). The inflowing river water could be a vector for the seed dispersal within one site but also on a wider scale through the runoff ditches. However, preliminary studies at the Queich meadows using seed traps in the meadows indicate little evidence for this theory as only few seeds could be trapped, probably due to the low water velocity (Buhk, data not shown). Irrigation positively influenced the preference for vegetative reproduction, too. Vegetative reproduction rises when the resource level increases and is highest at sites with a patchy mosaic-like distribution of intermediate and high fertility levels (Svensson et al. 2013). The increase in vegetative reproduction in irrigated meadows could thus be a result of the patchy sediment and water distribution within the meadows.

The responses of individual species within functional groups to irrigation were variable, indicating that the functional group response was amplified by the respective dominant species (hypotheses II). The individual response towards environmental influences on the species level are challenging for studies dealing with plant functionality. Especially for manipulation experiments using functional groups to explain their influence on ecosystem processes this result can be fairly important for the selection of species as representatives of certain functional groups.

Species composition

As expected the individual responses of plant species to irrigation and fertilization resulted in changes in the plant species composition. Explanations for the species-specific effects of irrigation on plants are similar to those for the functional groups (e.g. formation of small scale open patches favor light-demanding species, see above). Moreover, irrigation possibly reduces detrimental effects during summer droughts. The higher water and coupled nutrient availability might positively influence species which are sensitive towards dry conditions.

In contrast to the functional composition, fertilization had an effect on the species composition. This finding confirms the general observations of fertilization effects on plant species compositions (e.g. Tilman 1982, Honsova et al. 2007, Galka et al. 2005). Fertilization can decrease the niche dimensionality and change the competitive structure in the plant community (Harpole & Tilman 2007). In general, fertilization (especially N applications) enhances the cover of nitrophilous and tall growing (grass) species while it decreases understory species due to light competition (Hautier et al. 2009, Gaujour et al. 2012). In our study this is e.g. reflected by the positive relation of the nitrophilous grasses *Alopecurus pratensis* and *Elymus repens* and the forb *Heracleum sphondylium* to fertilization (Fig. 3b). To conclude, the relatively low nitrogen applications in our study system are sufficient to change the plant species composition (and also plant species richness, Rudolph et al., data not shown), but they had only minor effects on plant functional groups.

Conclusions

Traditional flood irrigation, and thus water availability, was the crucial factor shaping the species and functional composition of the hay meadows. In contrast to the effect of irrigation, we found comparatively weak effects of fertilization on functional composition. We conclude that irrigation benefits functionally complex vegetation assemblages by favoring legume and subordinate species, which may enhance the heterogeneity of the vertical vegetation structure. Moreover, differences in the response of overall and per-species cover of functional groups to irrigation underline the importance to consider species-level reactions to environmental factors in functional vegetation analysis.

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Supporting information to the paper

Appendix A

A. 1. Percent cover values (mean and SE) of sampled plant species in irrigated and non-irrigated meadows.

A. 2. Moran's I correlograms for the selected study sites

CHAPTER 3

CONTRASTING EFFECTS OF IRRIGATION AND FERTILIZATION ON PLANT DIVERSITY IN HAY MEADOWS

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Abstract

Extensive grassland management practices are crucial drivers to maintain biodiversity. However, it is challenging to combine biodiversity conservation with high agricultural yields. Traditional lowland meadow irrigation used to be a common management practice to improve hay production. However, it has been widely abandoned throughout Europe due to land use intensification. In an observational field study we examined the long-term impact of traditional irrigation, fertilization and biomass production on plant diversity of hay meadows. Traditional meadow irrigation enhanced plant alpha diversity (Simpson diversity and Evenness) and beta diversity (heterogeneity of multivariate dispersions). However, we found annual differences in the strength and significance of these effects, possibly due to different weather conditions. In contrast, plant species richness was unaffected by irrigation but consistently negatively influenced by the amount of applied N fertilizer. Moreover, we found significant relations between plant alpha diversity and biomass which were either unimodal (plant species richness and Simpson diversity) or negative (Evenness). Our results confirm the generally negative effects of fertilization on plant species richness. The moderately higher plant alpha and beta diversity in irrigated meadows may be a result of the heterogeneous within and between site environmental conditions induced by the annually repeated irrigation events. We conclude that traditional meadow irrigation is compatible with the conservation of plant diversity. Even stronger conservation benefits could be expected from diversified irrigation schemes that include longer-term inundation to favor even more hygrophilic plant communities.

Introduction

Semi-natural grasslands are key habitats for biodiversity conservation (Baur et al. 2006, Poschlod & WallisDeVries 2002) but have declined due to management intensification and abandonment within the past centuries (Poschlod, Bakker & Kahmen 2005, Wesche et al. 2012). In grasslands, plant species diversity and vegetation structure are mainly determined by soil nutrient availability, frequency and timing of mowing or grazing, natural and anthropogenic disturbances such as flooding, drought and fire as well as land improvement (Hopkins & Holz 2006). Extensive management practices are crucial drivers for biodiversity (Waldhardt et al. 2003, Kleijn et al. 2009). However, it is challenging to combine biodiversity conservation with efficient agricultural land-use (Tscharntke et al. 2012), as high biomass production in grasslands seems to entail low species richness (Guo 2007, Lamb 2008).

In Central Europe, land use patterns of extensive management have been developed over centuries and have thus shaped regional species and habitat assemblages. This makes it necessary to understand the impact of traditional management regimes on the regional biodiversity (Jongman 2002). Traditional grassland management regimes are characterized by no or low fertilizer applications, low stocking rates and late cutting and are frequently seen as the key for maintaining grassland biodiversity, which has become a primary goal of environmental policy (Muller 2002, Isselstein, Jeangros & Pavlu 2005). Agri-environment schemes promote traditional extensive grassland management to preserve biodiversity by compensation payments but their efficiency is questionable (Kleijn & Sutherland 2003, Humbert et al. 2012).

Lowland meadow irrigation using open water channels used to be common to improve hay production (moistening irrigation and fertilizing irrigation), soil temperature regulation and pest control (Leibundgut 2004, Schellberg 2005, Leibundgut & Kohn 2014a). These traditional irrigation systems have been widely abandoned throughout Europe due to the ongoing intensification of agriculture or have been replaced by e.g. sprinkler-irrigation systems (Hassler 1995, Crook & Jones 1999, Riedener, Rusterholz & Baur 2013, Leibundgut & Kohn 2014a). In Germany, irrigation history can be traced back to the 12th and 13th century (Endriss 1950) and had its prime time during the 19th century, where a relevant fertilization effect of irrigation is assumed because river water contained unfiltered sewage (Schellberg 2005). Irrigation techniques were adapted to the local conditions and historical development creating heterogeneous landscape patterns (Leibundgut & Kohn 2014a) possibly influencing biodiversity at larger spatial scales. Since then, water meadows in Germany decreased from about 250.000 ha to a few thousand hectares during the 20th century (Leibundgut 2004). The general character of these water meadows is largely replaced by areas of intensified agriculture and their naturally high biodiversity is degraded (Leibundgut 2004).

Meadow irrigation and fertilization can influence both the floristic composition and species richness through various factors. The impact of fertilization is well studied but results are manifold (Humbert et al. 2015): The reaction varies from unimodal (Kleijn et al. 2009) over linear decrease with rising nitrogen input (Suding et al. 2005) to exponential decrease in species richness (Kleijn et al. 2009). Mineral nitrogen fertilization promotes the growth of nitrophilous grass species and thus has a detrimental effect on plant diversity by competitive exclusion of less nitrophilous (Gaujour et al. 2009 and references therein) and understory species (Hautier, Niklaus & Hector 2009). Species with a low abundance are the first to disappear if meadows are fertilized with nitrogen (Suding et al. 2005, Kleijn et al. 2009), which has negative effects for plant species diversity (beta diversity). Irrigation management with frequent flooding and draining and the installation of the open water channels can shape mosaic-like vegetation patterns reflecting the varying soil-water conditions (Riedener, Rusterholz & Baur 2013, Hoppe 2012) and affecting plant diversity (Riedener, Rusterholz & Baur 2013, Andrey et al. 2014) as well as functional composition (Müller et al. 2015).

Both meadow irrigation and fertilization aim to increase biomass production (Leibundgut 2004). Intensively managed grasslands with high fertilization rates and high biomass production, however, go along with low species richness (Lamb 2008). The negative impact of fertilization on species diversity is well-studied whereas the long-term consequences of irrigation on both biodiversity and biomass production remain controversial (Hassler 1995 and references therein). Thus there is an urgent need for sustainable management strategies that bridge the gap between agricultural needs and the maintenance of grassland biodiversity.

Here, we aimed to analyze the role of traditional meadow irrigation for the plant species diversity at different scales and its linkage to fertilization and biomass production. In particular we addressed the following hypotheses: (i) Irrigation enhances plant alpha diversity whereas fertilization reduces species richness by promoting the dominance of few species. (ii) High levels of biomass production reduce species richness (iii) Plant beta diversity is higher in irrigated meadows than in non-irrigated meadows because irrigation management differed among irrigated meadows. (iv) Moreover, plant beta diversity is higher in unfertilized than in fertilized meadows due to the homogenization effect of fertilization.

Materials and methods

Study area and site selection

Our study area is located in the lowland of the river Queich between Landau and Lustadt (Rhineland-Palatinate, Germany; 49° 11′ 52.9″ N, 8° 7′ 34.2″ O). The annual average precipitation is 667 mm with a mean annual temperature of 10.5 °C (German Weather Service: stations Landau and Neustadt, reference period 1971-2000). Soils of the alluvial sediments are sandy to loamy (Briem & Geiger 2008). The study area is protected under the EU habitats directive as a part of the NATURA 2000 network. The meadows in the Queich lowland are mainly used for hay production. The irrigation history in this region started in the mid-15th century (Fiedler 1965) but suffered from a strong decline in the 1950s-1970s. Still, some of the meadows have been continuously irrigated since the 17th century. Additional water meadows have been reactivated within the scope of nature conservation within the last 15 years. The meadows are irrigated by a system of open water channels and weirs which lead the water from the nearby river into the meadow (lowland irrigation type; Leibundgut 2004). This leads to a relatively homogeneous water flow and prevents stagnant moisture (Hassler 1995). The inundation is kept up for two to three days. Then the weirs are opened and the remaining water flows back into the river through a drain ditch. The historical changes in meadow management strategies have created a mosaic of irrigated and formerly irrigated meadows with a half-extensive to half-intensive management (Dierschke & Briemle 2008).

We studied 33 hay meadows which differ in their irrigation status and fertilization treatment (n non-irrigated/unfertilized = 9, n non-irrigated/fertilized = 4, n irrigated/unfertilized = 8, n irrigated/fertilized = 12). We obtained management data (irrigation status, amount of N fertilization, grazing, and mowing) by personal interviews with the landowners and farmers. The irrigated meadows were irrigated three to four times per year. The fertilized meadows were fertilized with either NPK (nitrogen, phosphorous, potassium; Nitrophoska) or CAN (Calcium ammonium nitrate). For the fertilized sites the amount of the applied nitrogen was calculated from the amount of the respective fertilizer and ranged from 6.5 - 70 kg N * ha-1 * year-1. All meadows were mown usually two times per year and occasionally grazed with sheep during winter.

Plant survey

In each meadow we randomly selected three subplots (3 x 3 m, ntotal = 99) using ArcGIS (version 9.3, Environmental Systems Research Institute, Inc., CA, US). The subplots were installed keeping a buffer zone of at least 10 m to adjacent areas (edge strips, forest and ditches) to avoid edge-effects.

The vegetation was sampled twice in 2012 and 2013 (May and August). In each subplot all vascular plants were identified to species level (according to Wisskirchen & Haeupler 1998) and species cover (%) was estimated using a percentage scale estimation table (1-100%). Species with only one individual per subplot were marked as 0.1. For statistical analyses, data of the three subplots were combined by using the average species' cover and total species richness.

Aboveground plant biomass

The aboveground biomass was determined only in 2013. Biomass sampling was done before the first cut (May) and again before the second cut (August). At each time biomass sampling was done within three successive days and all standing biomass was clipped to 2 cm height in three 25 x 25 cm squares per subplot. The biomass was oven dried at 65 °C for 48 h. The dry weight of the biomass [g/m²] was determined and the sum of both sampling dates was used for further analyses.

Data Analysis

We combined spring and summer vegetation sampling data from each year by averaging the percent cover values for each subplot. We analyzed years separately because different weather conditions among years might lead to different effects of our treatments on the vegetation.

Alpha diversity measures (plant richness, Simpson diversity 1-D, Evenness) were related to the explanatory variables irrigation (binary variable: yes/no) and fertilization (continuous variable: amount of N ha/year) using linear models. Because of the potential polynomial relationship of diversity and fertilization the quadratic term of fertilization was also included into the models. In the models for 2013, biomass (continuous: g/m²) and the quadratic term of biomass, because of the assumed polynomial relationship of diversity and biomass (Kleijn et al. 2009), were additionally included as co-variables. Model residuals were checked visually for normality and homogeneity of variances using diagnostic plots (Zuur et al. 2009). Tests for significance were done with permutational ANOVA (command 'PermTest' in R library 'pgirmess'; Giraudoux 2014).

Comparisons of plant beta diversity between irrigated and non-irrigated and between fertilized and unfertilized meadows were done using the homogeneity of multivariate dispersions based on the Sørensen similarity of species presence-absence data (using the command 'betadisper' in the R package 'vegan') (Anderson, Ellingsen & McArdle 2006). Differences between the multivariate dispersions of the two respective meadow types were tested with ANOVA. All analyses were performed using R 3.1.2 (R Core Team 2014).

Results

Alpha diversity

Simpson diversity and Evenness of plants were higher in irrigated than in non-irrigated meadows (Fig. 1). However, for Simpson diversity this effect was significant only in 2013 (Table 1). Plant species richness was not affected by irrigation but decreased with increasing amount of fertilization in both years (Table 1, Figs 2A and B). Fertilization also had a negative effect on Simpson diversity, however, this pattern was only found in 2012 (Table 1, Fig 2C). In 2013, we found a significant relation of biomass with species richness, Simpson diversity and Evenness (Tab. 1). Both species richness and Simpson diversity showed a hump-shaped response and peaked at intermediate biomass values (Figs 3A and B), whereas Evenness decreased monotonously with increasing biomass (Fig. 3C).

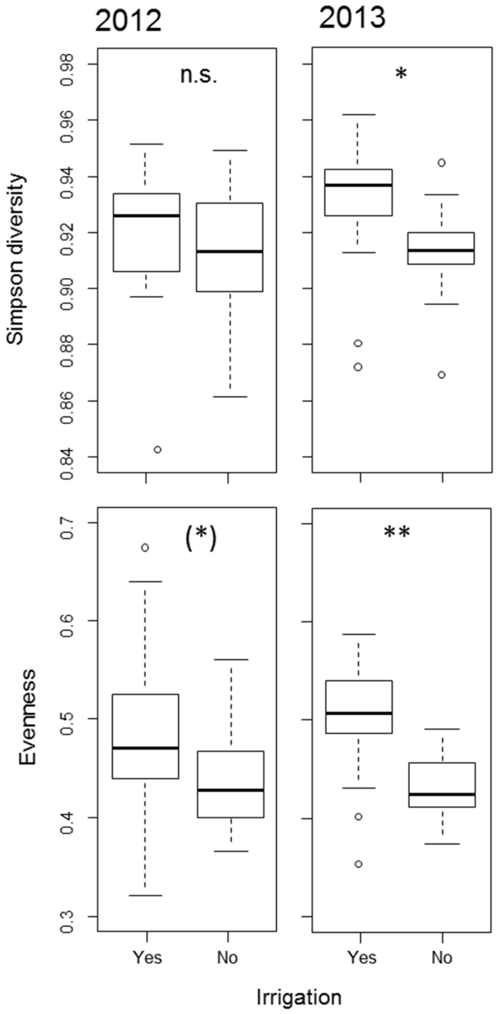

Fig. 1. Effects of meadow irrigation on Simpson diversity and Evenness of plants in 2012 and 2013. Significance was tested with linear models and permutational ANOVA (see Tab. 1). n.s. not significant, (*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$.

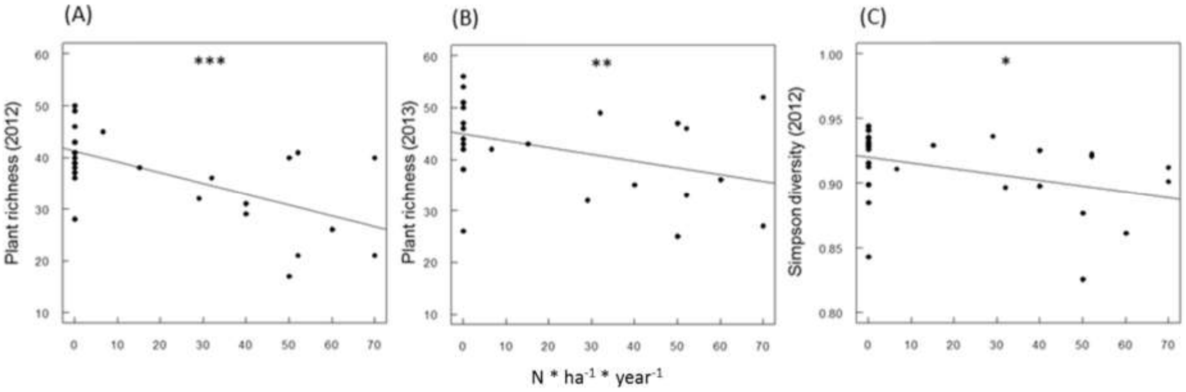

Fig. 2. Negative effects of fertilization (N * ha^{-1} * year^{-1}) on plant species richness in (A) 2012 and (B) 2013 and on (C) Simpson diversity in 2012 in traditional irrigated meadows. Significance was tested with linear models and ANOVA or permutational ANOVA (see Table 1). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Table 1. Relation of plant alpha diversity to irrigation (yes/no), fertilization (N * ha^{-1} * $year^{-1}$), and aboveground biomass (g/m²; only in 2013). Significance of explanatory variables was tested with permutational ANOVA.

Response	**Explanatory variables**	**Estimate**	**p**
2012			
Richness	Irrigation	-2.3059	0.339
	Fertilization	-0.3124	**0.001**
	Fertilization^2	0.0020	0.587
Simpson	Irrigation	0.0139	0.248
	Fertilization	-0.0008	**0.044**
	Fertilization^2	0.0000	0.691
Evenness	Irrigation	0.0630	*0.056*
	Fertilization	0.0001	0.345
	Fertilization^2	0.0000	0.952
2013			
Richness	Irrigation	0.6970	0.587
	Fertilization	-0.2293	**0.010**
	Fertilization^2	0.0018	0.314
	Biomass	1.6734	0.960
	Biomass^2	-0.0156	**< 0.001**
Simpson	Irrigation	0.0188	**0.034**
	Fertilization	0.0008	0.513
	Fertilization^2	-0.0000	0.804
	Biomass	-0.0025	*0.056*
	Biomass^2	-0.0000	**0.023**
Evenness	Irrigation	0.0567	**0.001**
	Fertilization	0.0046	0.267
	Fertilization^2	-0.0001	0.078
	Biomass	-0.0043	**0.011**
	Biomass^2	0.0000	0.431

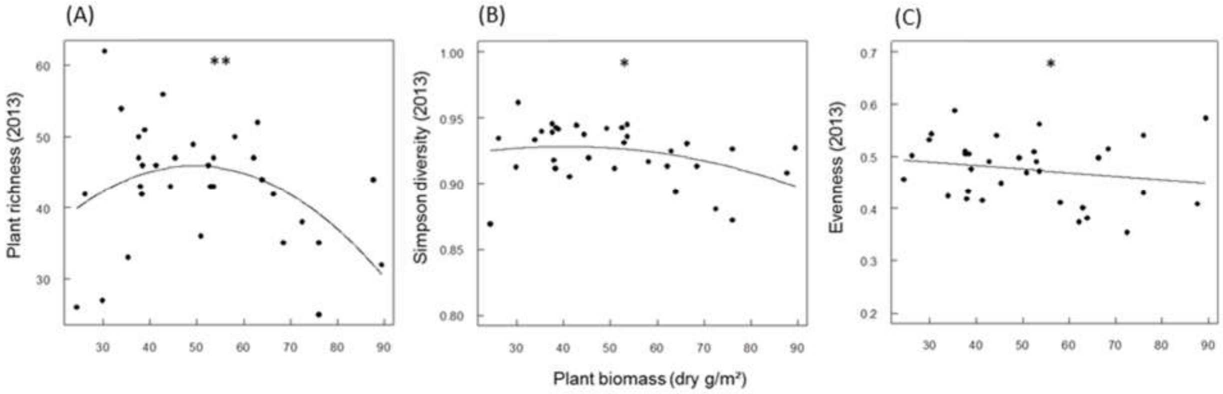

Fig. 3. Relationships between plant biomass and (A) plant species richness, (B) Simpson diversity and (C) Evenness in 2013 in traditional irrigated meadows. Significance was tested with linear models and ANOVA or permutational ANOVA (see Table 1). * $P < 0.05$, ** $P < 0.001$.

Beta diversity

Irrigation positively influenced plant beta diversity in 2012, i.e. the mean distances to the centroid were significantly higher in irrigated than in non-irrigated meadows (F1,31 = 5.2, P = 0.029) (Fig. 4a). In contrast, mean distances to the centroid did not differ significantly between irrigated and non-irrigated meadows in 2013 (F1,30 = 1.6, P = 0.213) (Fig. 4b).

Unexpectedly, fertilization had no significant influence on plant beta diversity. In both years the mean distances to the centroid did not significantly differ between fertilized and unfertilized meadows (2012: F1,31 = 1.8, P = 0.190; 2013: F1,31 = 1.2, P = 0.281) (Fig. 5).

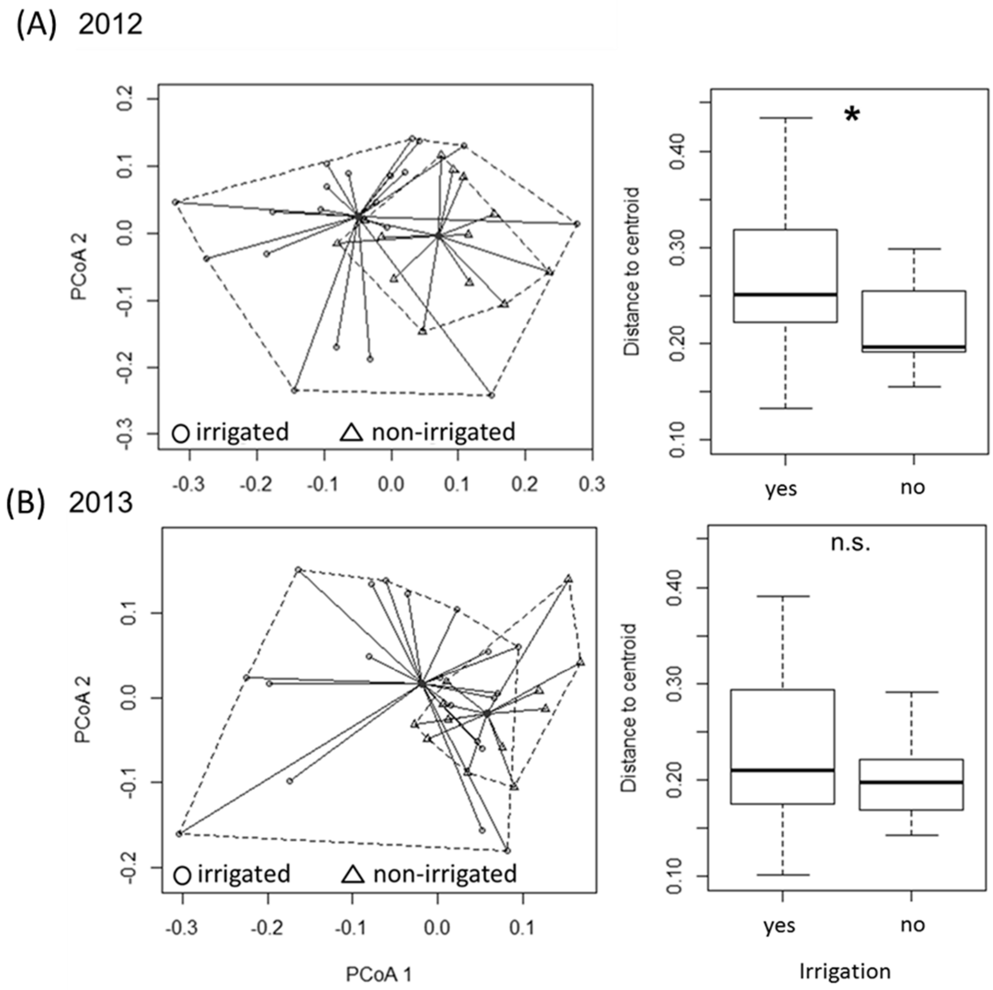

Fig. 4. Plant beta diversity (mean distance to centroid) of irrigated and non-irrigated meadows in (A) 2012 and (B) 2013. Differences were tested with homogeneity of multivariate dispersions (see text). n.s. not significant, * $P < 0.05$.

Discussion

Our results indicate positive effects of traditional meadow irrigation on plant alpha diversity (Simpson diversity, Evenness) and beta diversity. However, we found annual differences in the strength and significance of the observed effects, possibly due to different weather conditions. In contrast, plant species richness was consistently unaffected by irrigation and negatively influenced by fertilization. Our results show that traditional meadow irrigation is compatible with the conservation of species-rich grasslands and can enhance the heterogeneity of plant assemblages on a landscape scale.

Positive effect of irrigation on plant diversity

In line with our first hypothesis irrigation increased plant alpha diversity in terms of Simpson diversity (significant in 2013 only) and Evenness in 2012 and 2013. Both diversity measures take the distribution of species cover into account and not the number of species per se. In other words, irrigation leads to more evenly distributed cover among species within meadows, while non-irrigated meadows were characterized by similar species richness but higher dominance of certain species. The reduced dominance in irrigated meadows would be in accordance with the intermediate disturbance hypothesis (Grime 1973), with irrigation events preventing the competitive exclusion of subordinates by restricting the growth of otherwise dominant species. Alpha diversity may therefore be enhanced by the stimulated growth of subordinate species (e.g. rosettes or legumes) and a reduced grass cover (Riedener, Rusterholz & Baur 2013, Müller et al. 2015). Alternatively, the higher alpha diversity in irrigated meadows may be due to positive effects of irrigation on small-scale heterogeneity. Although the installation of main and drain ditches aims to provide an even flow of the irrigation water throughout the meadows, the water distribution is patchy depending on the micro-relief of the meadows (own observations, Hoppe 2012, Leibundgut & Kohn 2014b and references therein). Patches which are inundated for longer times than others can be expected to affect the competitive structure of the community by giving higher advantage to plants adapted to wetter soil conditions whereas patches that dry faster will foster the competitive abilities of plants which cope better with dryer soils (Pollack 1998). The long-term impact of irrigation on the plant species composition is discussed in Müller et al. (2015). Overall, small-scale habitat heterogeneity within irrigated meadows could explain the higher alpha diversity.

As hypothesized, we also found a higher beta diversity, expressed as the heterogeneity of multivariate dispersions, between irrigated meadows (significant in 2012 only). We explain this by the fact that irrigation is heterogeneous among sites in terms of the date of irrigation, the duration of the inundation (irrigation days per year) and possibly the amount of irrigation water which depends on the water load of the river and the position of the meadow in relation to the inflow. Moreover, irrigation may induce heterogeneous leaching of nitrogen depending on the water regime and soil conditions. These local specifications make generalizations concerning the impact of irrigation on plant species composition difficult (Leibundgut & Kohn 2014a).

Negative effects of fertilization on plant diversity

Our results confirm the generally negative effects of fertilization on plant species richness, particularly in grasslands (Gaujour et al. 2012 and references therein). Plant species richness was strongly reduced by the amount of applied nitrogen, though the negative influence of fertilization on Simpson diversity was only significant in the 2013 dataset. Resource limitation and the heterogeneous resource availability are described as the key for plant species coexistence following the niche dimension hypothesis (Harpole & Tilman 2007). Fertilization decreases niche dimensionality and thus causes a detrimental effect on plant diversity by changing the competitive structure in the community (Harpole & Tilman 2007). This leads to an increased growth of mainly nitrophilous grass species and thus induces competitive exclusion of less-nitrophilous and understory species that suffer from shading (Hautier, Niklaus & Hector 2009, Gaujour et al. 2012 and references therein). Rare species (in terms of abundance) are most likely to become locally extinct due to these changes in the dominance structure of the plant community (Suding et al. 2005, Kleijn et al. 2009).

Biomass and diversity relationship

We found significant relationships between aboveground biomass and plant alpha diversity. For plant species richness and Simpson diversity, the quadratic term of biomass was significant and underlines the hump-shaped or unimodal relation between biomass production and diversity, i.e. meadows with the lowest and highest biomass were characterized by the lowest diversity (Fig. 3; Tilman 1982, Rajaniemi 2003). However, even a linear negative response could be in line with this theory, because our sampled productivity gradient was relatively short ranging from (slightly below) medium to high (Mittelbach et al. 2001). This is supported by the marginally significant negative effect of the linear term on Simpson diversity and the significant linear decline of Evenness along the gradient, confirming higher dominance of certain grass species in the most productive meadows (Müller et al. 2015). Possibly, under low soil resource availability the competition for light does not play an important role but individuals compete for nutrients (Rajaniemi 2003). The more resources are available (either through fertilization or through irrigation), the higher is the competition for light (Rajaniemi 2003). However, if intermediate levels of soil resources are exceeded, competition for light due to dense biomass leads to species selection outcompeting smaller species (Hautier, Niklaus & Hector 2009) resulting in less even species compositions.

Differences between years

Some patterns varied between the two study years. Strong year-to-year changes in plant communities have been described by Thórhallsdóttir (1990) where for example tufted grasses like Holcus spp. tended to remain very stable between years while others like Trifolium spp. changed their position between years. Stampfli and Zeiter (2004) name drought events to be responsible for shifts in vegetation composition between years. We assume that in our study the dry weather in February to April 2012 (three-months sum of the water balance: -140 mm; weather station Herxheimweyer, Dienstleistungszentrum Ländlicher Raum RLP) as compared to the more typical year 2013 (three-months sum of the water balance: + 2.1 mm; weather station Herxheimweyer. Dienstleistungszentrum Ländlicher Raum RLP) might be responsible for some year-to-year differences, possibly in interaction with herbivore pressure (Rees & Brown 1992). Among the dominant moisture-dependent species, *Alopecurus pratensis*, *Holcus lanatus* and *Ranunculus repens* increased strongly from 2012 to 2013 in non-irrigated, but not in irrigated meadows. This confirms that the vegetation of non-irrigated meadows was strongly influenced by the dry conditions in spring 2012. The observed between-year variability underlines the need for multiple year data collection to adequately describe the spatial vegetation pattern (Bakker et al. 1996).

Conclusions

Our study confirms the reduction of plant species richness through grassland fertilization. In contrast, traditional meadow irrigation had moderate positive effects on plant alpha (Simpson and Evenness) and beta diversity. However, the effect sizes differed between study years and the positive effects were not consistently significant. This underlines the importance of long-term studies. We conclude that traditional meadow irrigation is compatible with biodiversity conservation in European grasslands. It requires low financial input and might thus be an interesting option for biological conservation, even if benefits to arthropods were less clear than to plants (Schirmel et al. 2014). Moreover, irrigation may be beneficial for famers by improving both biomass production (Cook et al. 2004, Stearne & Cook 2013) and forage quality (Leibundgut & Kohn 2014a). The current irrigation schemes in our study area are adapted to the maintenance of mesophilic Arrhenaterion grasslands and are applied relatively uniformly across the study region. We expect that a diversification of irrigation schemes, with longer-term inundation on selected sites within the landscape would yield much higher conservation benefits by favoring more hygrophilic plant communities.

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Supporting information to the paper

Appendix B

B. 1. Percent cover values (mean and SE) of sampled plant species in irrigated and non-irrigated meadows (2013 and 2013).

B. 2. Effects of irrigation on plant α-diversity.

CHAPTER 4

EFFECTS OF TRADITIONAL FLOOD IRRIGATION ON INVERTEBRATES IN LOWLAND MEADOWS

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Abstract

Lowland meadow irrigation used to be widespread in Central Europe, but has largely been abandoned during the 20th century. As a result of agri-environment schemes and nature conservation efforts, meadow irrigation is now being reestablished in some European regions. In the absence of natural flood events, irrigation is expected to favour fauna typical of lowland wet meadows. We analysed the effects of traditional flood irrigation on diversity, densities and species composition of three invertebrate indicator taxa in lowland meadows in Germany. Unexpectedly, alpha diversity (species richness and Simpson diversity) and beta diversity (multivariate homogeneity of group dispersions) of orthopterans, carabids, and spiders were not significantly different between irrigated and non-irrigated meadows. However, spider densities were significantly higher in irrigated meadows. Furthermore, irrigation and elevated humidity affected species composition and shifted assemblages towards moisture-dependent species. The number of species of conservation concern, however, did not differ between irrigated and non-irrigated meadows. More variable and intensive (higher duration and/or frequency) flooding regimes might provide stronger conservation benefits, additional species and enhance habitat heterogeneity on a landscape scale.

Introduction

Semi-natural grasslands are key habitats for biodiversity conservation and an integral part of the Central European cultural landscape [1–3]. They are among the most species-rich habitats and serve as refuges for several rare and endangered species [2–4]. Regular disturbance due to traditional management permits the coexistence of numerous species in semi-natural grasslands [2]. During the last decades however, semi-natural grassland have dramatically declined in Central Europe and further declines to less than 50% of the current area are predicted [5,6]. Major causes are agricultural intensification and the abandonment of traditional management. The latter is mainly due to the reduced cost-effectiveness of traditional land use practices [5,7]. Agricultural intensification practices for seminatural meadows include higher fertilizer and herbicide applications, earlier and more cuts per year, and the use of modern mowing techniques [8]. This results in eutrophic, structurally poor, and homogeneous meadows with negative impacts on diversity, species composition, and ecosystem processes [9].

Until the early 20th century, meadow irrigation was widespread in Central Europe to increase hay yield [10]. For example, around 1900 in some regions of Germany, irrigated meadows made up about 60% of the total grassland [11]. The main effects of irrigation were nutrient input, topsoil humidification, and extension of the vegetation period. Nowadays irrigation practices are mostly abandoned and traditionally irrigated meadows with their associated species are restricted to few remnant areas [12]. Thanks to agri-environment schemes (e.g. in form of compensation payments), nature conservation efforts, and due to mitigation and compensation measures, the traditional irrigation practices could be maintained or re-established in some European regions [13]. However, the value of agri-environment schemes is under debate and further analyses of management strategies are necessary [14,15]. Therefore, it is of growing interest to determine, how traditional irrigation practices affect biological diversity. In this context, Riedener et al. [16] recently showed that changes in irrigation techniques have influenced some aspects of plant and gastropod diversity in Swiss mountain hay meadows. However, knowledge of the influence of traditional meadow irrigation on invertebrate diversity and composition is still poorly understood, and this is especially true for flood irrigation in lowland regions.

The objective of this study was to analyse whether traditional flood irrigation in lowland meadows has an effect on invertebrate diversity and species composition. Irrigation is assumed to create small-scale differences in moisture and sediment conditions which may increase microhabitat and vegetation heterogeneity [16]. In accordance to the habitat-heterogeneity-hypothesis irrigation might therefore have positive effects on local species richness [17–20]. Moreover, flood irrigation in our study area is conducted in a similar way among irrigated sites, but differs in timing and intensity. This may lead to non-uniform moisture conditions among irrigated meadows with heterogeneous species compositions and higher beta diversity. To investigate these predictions we conducted a field survey in the 'Queichtal' in Rhineland-Palatine, Germany. We compared traditionally flood-irrigated meadows with meadows, where there has been no irrigation for at least thirty years. We focused on orthopterans, carabids and spiders, which are found at different trophic levels within grassland foodwebs and occur in different vegetation layers. Orthopterans (Orthoptera) are mostly grass-dwelling herbivores, where they are often both the main invertebrate consumers and the main food source [21]. Most carabids (Coleoptera: Carabidae) are grounddwelling predators, but some are scavengers and herbivores [22]. Spiders (Araneae) inhabit both the ground and field layer, often in high abundances, and are predatory [23]. All three arthropod groups have been used as indicators of ecosystem conditions and habitat quality (orthopterans: [24,25]; carabids: [26,27]; spiders: [28,29]).

We addressed the following hypotheses: (i) Flood irrigation increases the local diversity of orthopterans, carabids, and spiders compared to non-irrigated lowland meadows. (ii) Flood irrigation leads to higher beta diversity relative to non-irrigated meadows. (iii) Flood irrigation shifts species assemblages towards more moisture-dependent species and those of higher conservation concern than species in non-irrigated meadows. Based on our findings we discuss if traditional flood irrigation can be useful for conserving biodiversity of semi-natural grassland species.

Materials and Methods

Ethics statement

Invertebrates were collected with the permission 42/553-254 from the Struktur- und Genehmigungsdirektion Süd (federal state authority of Rhineland-Palatine, Germany). Additionally, we obtained permissions from all private farmers and landowners to conduct the field work on their meadows.

Study sites

The study was conducted in 2012 in the 'Queichtal' in the Upper Rhine valley in Rhineland-Palatine, Germany (Fig. 1).

With a length of 51 km, the river Queich is an important drainage system of the adjacent low mountain range 'Pfälzerwald' into the Rhine. Soils of the alluvial sediments are sandy to loamy [30]. Annual mean temperature in this region is 10.5uC (station Neustadt) and annual mean precipitation is 667 mm (station Landau; German Weather Service). The studied section of the Queichtal covers about 700 ha, is part of the NATURA 2000 network, and is thus protected by the EU habitats Directive [31].

Due to the predominance of moist soils with low cation availability, land use in the Queichtal is dominated by forest and grassland with different management and irrigation regimes. The formerly widespread traditional flood irrigation of lowland meadows was almost totally abandoned after the Second World War and is nowadays only applied in a few remnant areas. For flood irrigation the water of the river Queich (or the tributaries 'Spiegelbach' and 'Fuchsbach') is dammed by weirs (Fig. 1) and delivered to the meadows by open ditches where it slowly flows over the ground ('lowland irrigation type'; [10]). Meadows are irrigated on average four times per year between April and August and each irrigation event lasts for 1–3 days.

A total of 32 meadows were selected stratified to meadow irrigation practice (yes or no) and fertilization (yes or no) (Table S1). Half of the meadows were traditionally irrigated and days of irrigation ranged from 4 to 12 days per year. On the other 16 meadows irrigation ceased more than 30 years ago. Half of the irrigated and not irrigated meadows were fertilized (with a maximum of 60 kg $N*ha^{-1}N*yr^{-1}$). Meadows were normally mown twice per year and extensive winter grazing by sheep occured on all meadows.

On each meadow we selected a 50650 m plot with a minimum distance of 100 m from the nearest plot and 10 m to the next ditch to minimise edge effects. Irrigated and non-irrigated meadows did not differ significantly in mean distance to the nearest forest (t-test: t30 = 0.563, P =0.578) and to the nearest permanent water (t-test: t30 = 0.529, P= 0.601). Permanent water was defined as any standing and flowing water body which permanently contained water.

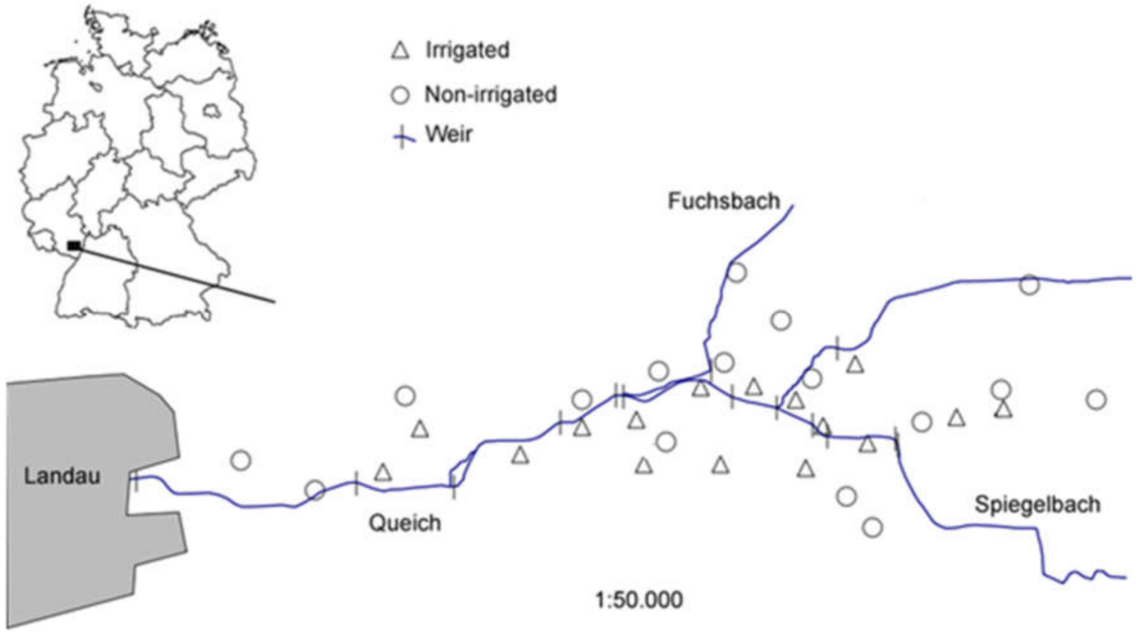


Fig. 1. Position of the study area 'Queichtal' in Germany (small figure) and of the 32 study sites.

Management and environmental parameters

Land use data on irrigation practice (yes or no) and fertilization (yes or no) were collected through on-site observations and interviews with landowners and local farmers. Plant species were recorded in three randomly selected 363 m subplots per plot in May/June before the first cut (unpublished data). For subsequent analyses, data of the three subplots were averaged and we calculated the unweighted mean Ellenberger indicator values for moisture (in the following 'humidity' to avoid confusion with animal species moisture indicator values) and nitrogen for a description of local habitat conditions. As species can be influenced by patch isolation [32], we calculated the distance (m) to permanent water and to forest for each sampling location in Google Earth [33].

Invertebrate sampling

Orthopterans were sampled once per plot during their main activity period in August with a box-quadrat. The box-quadrat is a very effective method for sampling orthopteran densities [34]. The box-quadrat we used had an area of 2 m^2 (1.4161.41 m) with white gauze-covered sides of 0.8 m height and was randomly dropped at 20 different locations per plot (total sampled area = 40 m^2 per plot). Collected individuals were determined to species level directly in the field using Bellmann [35] and then released. Carabids and spiders were sampled using pitfall traps (6.5 cm in diameter, 7 cm deep) filled to one third with a 50% propyleneglycol solution. Per plot, four pitfall traps (N = 160 traps) were randomly installed with a minimum distance of 5 m to each other. Traps were exposed for two sampling periods from 03 to 24 April and again from 12 to 28 June.

Carabids and spiders were determined to species level using the identification keys of Müller-Motzfeld [36] (carabids) and Roberts [37] (spiders). The four traps per plot were treated as a unit and data from both sampling periods were combined to obtain one dataset for further analyses. Due to loss and damage of some pitfall traps, we finally included 28 plots (N = 14 per meadow type each with N= 7 fertilized) in the data analyses of carabids and spiders.

Data analysis

Species were classified as species of conservation concern when they were listed in regional red lists (all species belonging to the categories ‘1’, ‘2’, ‘3’, ‘4’, and ‘V’; orthopterans: [38]; carabids: [39]; spiders: [40]). For species moisture dependence we used published moisture indicator values. For orthopterans, transformed moisture values were obtained from Maas et al. [41] (Table S2). The values range from ‘1’ (strongly xerophilic) to ‘5’ (strongly hygrophilic). For carabids, moisture values range from ‘0’ (most xerophilic) to ‘9’ (most hygrophilic) according to Irmler and Gürlich [42]. For spiders, we used the moisture values of Entling et al. [43]. For a better comparison to the other taxa we transformed values by 12x, i.e. species with the lowest value ‘0’ are most xerophilic and species with the highest value ‘1’ are most hygrophilic. For each species we calculated the spearman rank correlation coefficient between species density and irrigation to express their ‘species irrigation affinity’ for our study area. Relationships between species irrigation affinities and species moisture indicator values (based literature data) were analysed using linear models.

The effect of irrigation on species richness and densities of orthopterans, carabids, and spiders were analysed using Poisson GLM’s for count data. Similarly, the irrigation effect on the combined number of species of conservation concern of all taxa (N = 28 sites) was analysed. In cases of overdispersion, we corrected the standard errors using a quasi-GLM model [44]. Differences in Simpson diversity (12D) between irrigated and non-irrigated meadows were tested with non-parametric Wilcoxon rank sum test, because assumptions for a t-test were violated. Community differentiation (beta diversity) among irrigated and non-irrigated meadows was analysed using the homogeneity of multivariate dispersions based on the Sørensen similarity of species presence-absence data (using the command ‘betadisper’ in the R package ‘vegan’) [45]. For each taxon, an ANOVA was used to test for differences between the multivariate dispersions of both meadow types.

Effects of the management and environmental variables on species composition of orthopterans, carabids, and spiders were analysed with a permutational multivariate ANOVA (command ‘adonis’ in R package ‘vegan’; [46]). Predictor variables were the two factors irrigation (yes or no) and fertilization (yes or no), the two local habitat parameters humidity and nitrogen (mean Ellenberger indicator values), and the two landscape parameters distance to permanent water and distance to forest. As a distance measure the Bray-Curtis distance was used. Significance of environmental variables was tested with permutation tests (999 permutations) with pseudo-F ratios. Variation of species compositions were visualised using nonmetric multidimensional scaling (NMDS) with the command ‘metaMDS’ in R package ‘vegan’. Again, the Bray-Curtis distance was used as a distance measure. All statistical analyses were done in R 2.12.2 [47].

Results

General results

A total of 7 orthopteran species (528 individuals), 47 carabid species (1,410 individuals), and 56 spider species (6,347 individuals) were found (Tables S32S6). All 7 orthopteran species were detected in both meadow types (Fig. 2a). A total of 40 carabid species were found in irrigated meadows compared to 32 species in non-irrigated meadows (Fig. 2b). In total 49 spider species could be detected in irrigated and 46 species in non-irrigated meadows (Fig. 2c).

Local diversity

There was no significant effect of irrigation on species richness of orthopterans ($z = 0.098$, $P = 0.922$, Fig. 2a), carabids ($t = 1.950$, $P = 0.051$; Fig. 2b), and spiders ($z = 1.407$, $P = 0.160$, Fig.

2c). While densities of orthopterans (t= 0.130, P= 0.898, Fig. 2d) and carabids (t= 1.484, P= 0.150, Fig. 2e) did not significantly differ between both meadow types densities of spiders were significantly higher in irrigated meadows (t= 3.266, P =0.003, Fig. 2f). Similar to species richness, Simpson diversity did not differ for orthopterans (W30 = 147.5, P= 0.4731, Fig. 2g), carabids (W26 = 62, P =0.104, Fig. 2h), and spiders (W26 = 87, P =0.629, Fig. 2i).

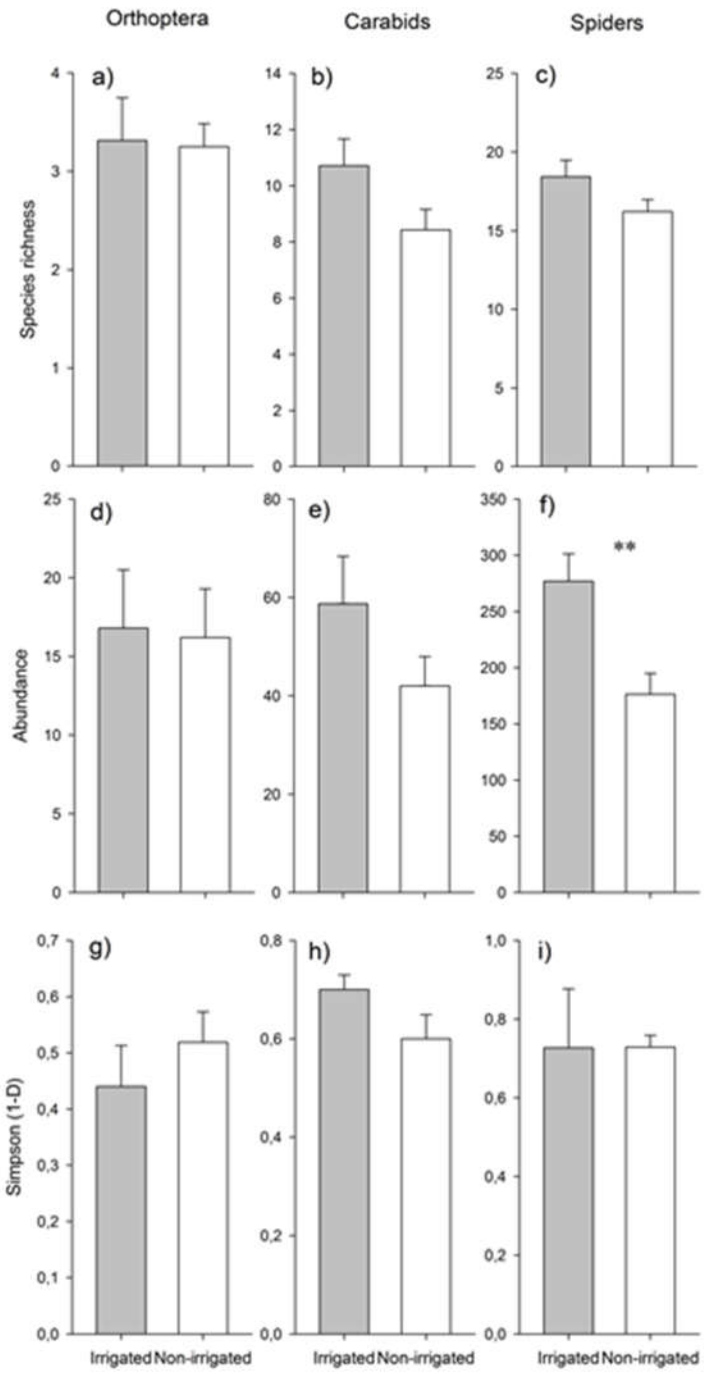


Fig. 2. Comparison of species richness (a–c), densities (d–f), and Simpson diversity (g–i) of orthopterans, carabids, and spiders between irrigated and non-irrigated meadows (mean and SE). Differences of species richness and densities were tested with Poisson GLM's and of Simpson diversity (12D) with non-parametric Wilcoxon rang sum tests.

Community differentiation (beta diversity)

Beta diversity (multivariate dispersion) of all investigated taxa was not influenced by irrigation. Mean distances to centroids did not differ significantly between irrigated and non-irrigated meadows for orthopterans (F= 1.237, P= 0.275, Fig. 3a), carabids (F =0.287, P= 0.596, Fig. 3b), and spiders (F= 4.023, P =0.055, Fig. 3c).

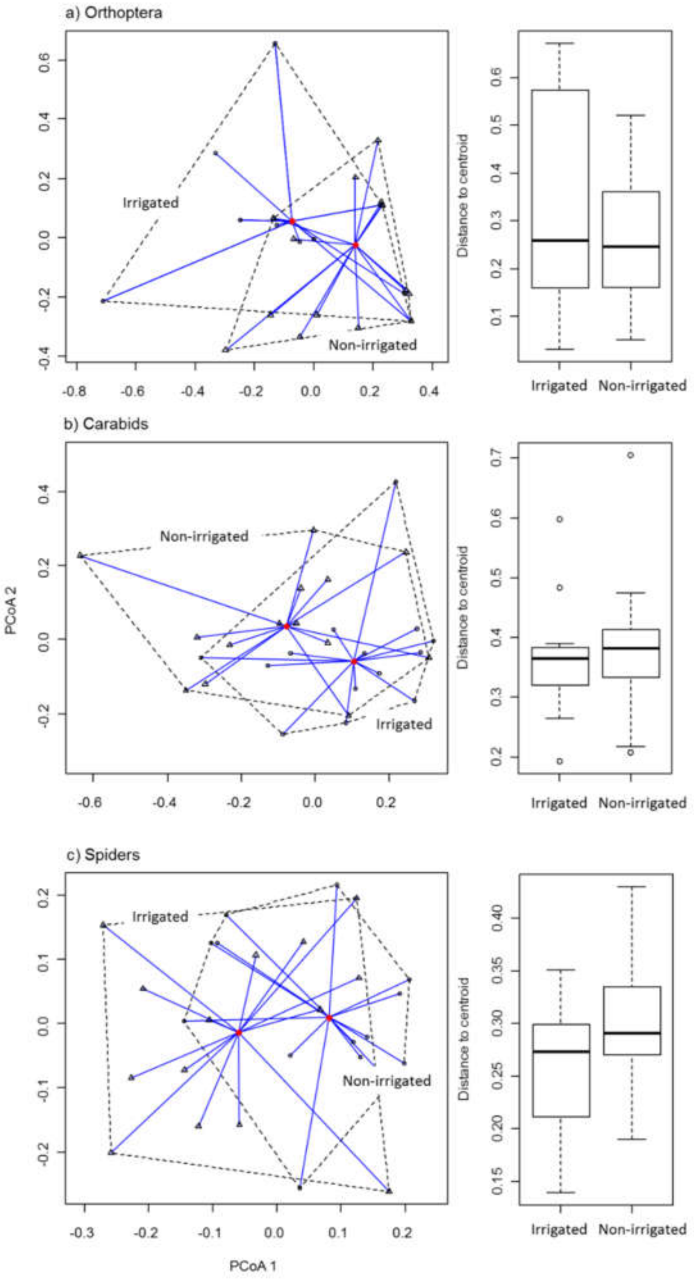


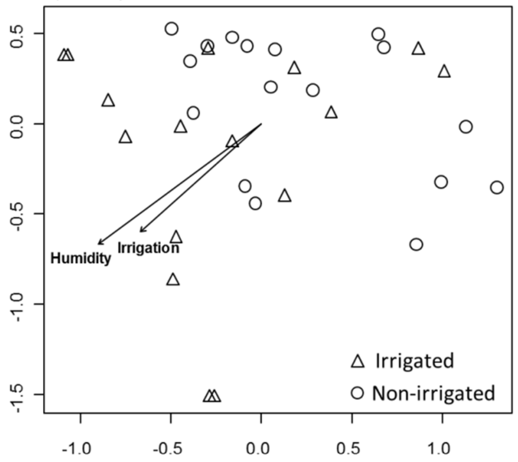
Fig. 3. Beta diversity (multivariate homogeneity of dispersions) of a) orthopterans, b) carabid and c) spider assemblages of irrigated and non-irrigated meadows. Distances (Sørensen similarity) are reduced to principal

coordinates and distances to group centroids (irrigated or non-irrigated) are shown. Differences of mean distances between meadow types were tested by ANOVA.

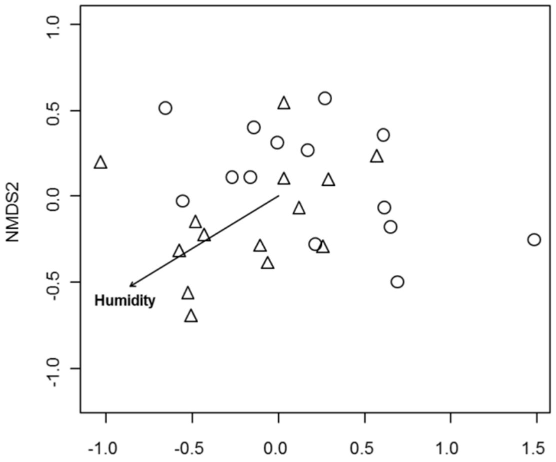
Species composition

Irrigation (yes or no) and humidity were the only variables having a significant effect on species composition, while fertilization, nitrogen availability, distance to permanent water and distance to forest had no effect (Table 1, Fig. 4). Orthopteran species composition was significantly affected by irrigation (F =2.51, R^2 = 0.073, P= 0.019) and humidity (F =2.93,R^2 = 0.085, P =0.011). Carabid species composition was affected only by humidity (F =2.49, R^2 = 0.088, P= 0.024) while spider species composition was influenced by irrigation (F =2.31, R^2 = 0.080, P= 0.041). As hypothesised, irrigation favoured the occurrence of moisture dependent species. For carabids (r = 0.48, P= 0.002, Fig. 5b) and spiders (r = 0.44, P,0.001, Fig. 5c) there was a significant positive relationship between species irrigation affinity (expressed as the spearman rank correlation coefficient) and species moisture indicator value. For orthopterans no significant relationship was found, however this may be a result of the low number of N= 7 species (Fig. 5a). The combined number of species of conservation concern of all three taxa did not differ between irrigated (3.660.6) and non-irrigated (2.460.3) meadows (z = 1.853, P= 0.064).

a) Orthoptera



b) Carabids



c) Spiders

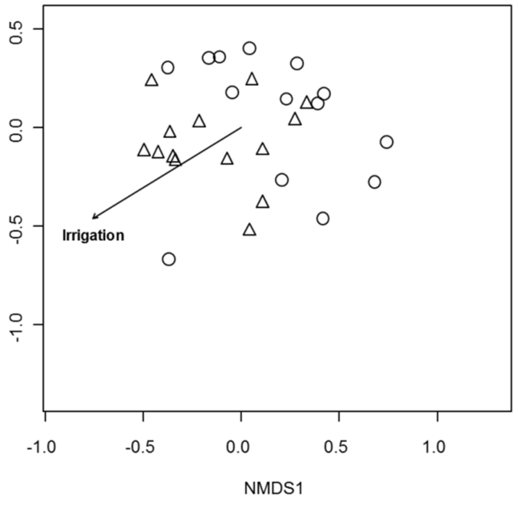


Fig. 4. NMDS ordinations of a) orthopterans, b) carabid and c) spider species composition of irrigated and non-irrigated meadows. Only significant environmental variables are shown (permutational multivariate ANOVA, for statistics see Table 1).

Tab. 1: Effect of environmental variables on species composition of Orthoptera, carabids, and spiders in irrigated and non-irrigated meadows in the Queichtal, Germany. Significance was tested by permutational multivariate ANOVA (command ‘adonis’ in R package vegan). Significant results ($P < 0.05$) are shown in bold.

	Orthoptera		**Carabids**		**Spiders**	
	R^2	P	R^2	P	R^2	P
Factors						
Irrigation (yes or no)	0.078	**0.019**	0.050	0.171	0.080	**0.041**
Fertilization (yes or no)	0.028	0.451	0.012	0.976	0.023	0.710
Habitat parameters						
Humidity	0.085	**0.011**	0.088	**0.024**	0.060	0.102
Nitrogen	0.023	0.568	0.029	0.582	0.033	0.451
Landscape parameters						
Distance to water	0.032	0.370	0.048	0.175	0.012	0.924
Distance to forest	0.031	0.405	0.027	0.613	0.061	0.121

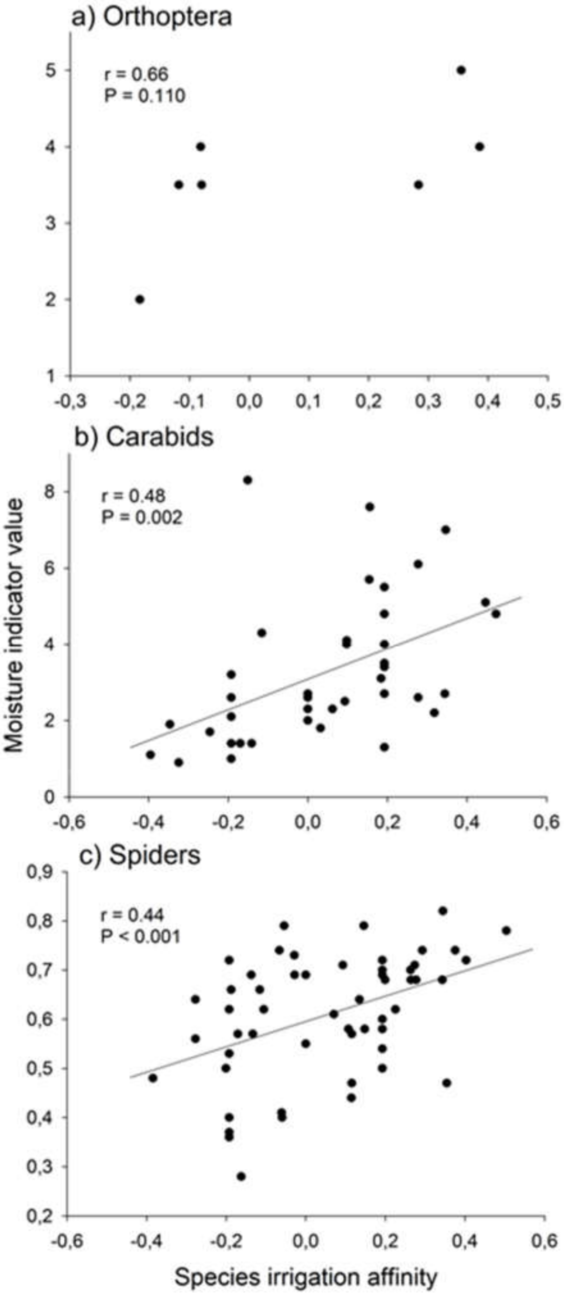


Fig. 5. Relationship between species irrigation affinity (spearman rank correlation coefficient of species densities to irrigation) and moisture indicator value of a) orthopterans, b) carabids, and c) spiders.

Discussion

Unexpectedly, traditional flood irrigation had no significant effect on diversity and species of conservation concern of orthopterans, carabids, and spiders in lowland meadows. However, flood irrigation and the associated environmental parameter humidity influenced the species composition of all taxa and shifted species assemblages towards more moisture-dependent species.

Local diversity

We assumed that traditional flood irrigation leads to small-scale differences in moisture and sediment conditions and consequently higher microhabitat and vegetation heterogeneity resulting in increased local diversity [16, 48]. However, in contrast to our hypothesis, traditionally flood irrigated meadows did not contain a higher local diversity (in terms of species richness and Simpson diversity) of orthopterans, carabids, and spiders compared to nonirrigated meadows. Possibly, the traditional irrigation system in our study area - on average four flooding events with a maximum of twelve irrigation days between April and August - is not sufficient to induce (measurable) heterogeneity effects. Riedener et al. [16] assumed that effects of the irrigation technique on diversity are only effective in combination with other management factors such as mowing and grazing regimes. Additionally, landscape variables such as patch isolation can influence species [32]. We accounted for possible confounding effects of management (mowing frequency, fertilization) and landscape parameters (distance to permanent water, distance to forest), none of which differed significantly between irrigated and non-irrigated meadows. However, as in any observational study, we cannot rule out that additional unmeasured management or environmental parameters have influenced our results.

In the literature, several studies in riparian habitats were able to detect positive effects of (natural) flooding on diversity [48–51]. However, in contrast to our study system with no (non-irrigated) and low intensive (irrigated) flooding, flood intensities in these studies are mostly studied along gradients containing higher intensities. Gerisch et al. [50] found positive effects for carabids at the river Elbe (Germany) and explained this by higher resource diversity in frequently flooded habitats. At the river Meuse (Belgium/Netherlands), Lambeets [50] could show that flooding initially had a positive effect on carabid diversity, which peaked at intermediate flooding degrees. This is in line with findings of Pollack et al. [48] in riparian meadows where plant species richness was highest at intermediately flooded river banks because of increased microhabitat heterogeneity.

Similar to diversity, densities of orthopterans and carabids did not differ between meadow types. However, spider densities were higher in irrigated meadows. One explanation might be enhanced food availability, because short time flooding can enhance soil organisms [52], which present important food source especially for linyphiid spiders [53].

Community differentiation (beta diversity)

Irrigation did not influence community differentiation and, in contrast to our hypothesis, beta diversity of orthopterans, carabids, and spiders was not higher in irrigated compared to non-irrigated meadows. Although flood irrigation between irrigated meadows differed in time and intensity, these differences were obviously too weak to result in more diverse species assemblages. Moreover, the traditional flooding method in the region - where the dammed river water slowly streams into the meadows and back into the river through a system of open ditches - leads to a relatively homogenous water flow. This prevents stagnant moisture [12] and moisture conditions on irrigated sites might be more uniform than expected. Human-altered repetitive flood events are known to result in uniform species compositions due to a homogenization of habitat structure [54, 55].

Species composition

As hypothesized, meadow irrigation and the associated altered humidity conditions influenced species composition of orthopterans, carabids, and spiders. Irrigation may therefore increase beta diversity at the landscape scale and contribute to diverse grassland communities. Assemblages of irrigated meadows contained more moisture-dependent species compared to non-irrigated ones. This was reflected for carabids and spiders by the positive relationships between species irrigation affinity and their moisture indicator value. For orthopterans this effect was not significant (most likely because of the low number of species), but the two species with the highest moisture indicator value – *Mecostethus parapleurus* and *Stetophyma grossum* – were significantly more abundant in irrigated meadows (Table S3). For all three taxa, humidity is known to be one of the most influencing environmental parameter structuring species compositions [27, 43, 56]. Impacts of (natural) flood disturbance on species and trait composition of orthopterans were previously shown by Dziock et al. [57]. Bonn et al. [48] found that flood regime strongly influenced carabid species assemblages, which was also found by Lambeets et al. [50] for carabid and spider communities. Although fertilization can strongly influence arthropods [58, 59] we could not detect an effect of fertilization. In general, fertilization application rates were low in the study area (0 to 60 kg N*ha^{-1}N*yr^{-1}), a range in which also plants showed no significant decrease in species richness (unpublished data). Similar to fertilization, the landscape parameters, distance to forest and to permanent water, did not differ between irrigated and non-irrigated meadows and had no effect on species compositions, respectively.

In contrast to our hypothesis, species compositions of flood irrigated meadows did not contain more species of conservation concern than non-irrigated meadows. This is in contrast to Bonn et al. [49] and Lambeets et al. [51], where anthropogenic alterations in flooding regimes not only have a strong influence on arthropod communities but also on the distribution of rare (and often endangered) riparian species. Again, this difference may be due to the low irrigation intensity in our study system.

Conclusion

Flood irrigation had no significant effect on local and beta diversity of orthopterans, carabids, and spiders in lowland meadows. In contrast, flood irrigation clearly changed species assemblages towards moisture-dependent species and probably increased beta diversity at the landscape scale. However, these species were mostly common species and assemblages of irrigated meadows did not contain more species of conservation concern compared to non-irrigated ones. More variable and intensive (higher duration and/or frequency) flooding regimes are likely to provide much stronger conservation benefits. Moreover, beneficial effects of flood irrigation might be more pronounce along the irrigation infrastructures (open ditches, drains, weirs) than in the open meadow, which will be tested in further studies.

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Supporting Information to the paper

Appendix C

C. 1. Moisture indicator values of Orthoptera.

C. 2. Abundances (mean and SE) of Orthoptera, carabid, and spider species in irrigated and non-irrigated meadows.

C. 3. Site characteristics of irrigated and nonirrigated meadows in the ‘Queichtal’, Germany. For explanations see text.

C. 4. Additional data.

CHAPTER 5

EXPERIMENT(S) ON THE EFFECT OF TRADITIONAL FLOOD IRRIGATION ON THE AVAILABILITY OF PLANT NUTRIENTS FOR CENTRAL EUROPEAN GRASSLAND SPECIES

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Abstract

The planetary boundary for the use of nitrogen has already been surpassed. Nevertheless we are forced to find sustainable management options to further reduce fertilizer N input and maintain primary productivity at the same time. Grassland flood irrigation used to be a widespread management option for the optimization of biomass production and is less harmful for biodiversity than fertilization. Thus, grassland irrigation could bridge the gap between agricultural demands and biodiversity protection. Plant nutrient availability was tested before during and after irrigation in a mesocosm experiment with three temperate grassland species. N_2O emission rates were used as a proxy for the N use efficiency of the respective plant species. Field measurements of nutrient availability and N_2O emissions were performed under *Holcus lanatus* in differently managed grassland (irrigation and fertilization). Our study revealed a positive effect of irrigation on NO_3 availability whereas the increased availability of other macro- and micronutrients was restricted to the day of irrigation. The increase in NO_3-availability was only fairly long-term under *Holcus lanatus* whereas *Centaurea jacea* and *Polygonum persicaria* recorded greater losses of all nutrients after irrigation. Redox-sensitive nutrients showed a significantly higher increase in their availability during irrigation than non-sensitive nutrients. N_2O emission rates showed the characteristic patterns for dry-wet-dry cycles but depended significantly on above- and belowground biomass which were species-specific. Field data showed comparable patterns although the effects were not as strong. Traditional meadow irrigation could be a management option to enhance nutrient availability on a short-term scale during drier periods and critical growth stages. However, fertilizer application and irrigation must be timed efficiently to support the effect of irrigation. Species-specific effects seem apparent and would need further insight, not to have a negative effect on biodiversity.

Introduction

One of the major threads to all ecosystems is the overuse of nitrogen (N) fertilizers. In the planetary boundary concept the point of no return already has been surpassed for the nitrogen cycle (Rockström et al. 2009; Steffen et al. 2011). Thus, agriculture faces the dilemma of having to decrease N fertilizer inputs on the one hand and keeping productivity high on the other hand. Globally as well as locally more N is applied than crops are taking up. The surplus N accumulates in non-target ecosystems causing detrimental effects on all affected ecosystems (Aber et al. 1995, Vitousek et al. 1997, Rabalais 2002). This unnecessary surplus leads to a multitude of environmental risks and has to be reduced. Almost all well recognized environmental hazards of the past decades are also related to N, which are (a) eutrophication of lakes, (b) acid rain (HNO_3^+), (c) ozone layer depletion (N_2O), (d) climate change (N_2O) and (e) groundwater contamination (NO_2^-). Moreover, fertilization (Clark & Tilmann 2008, Gaujour et al. 2012) as well as atmospheric N depositions (Stevens et al. 2004) widely lead to reduced biodiversity in grassland and other ecosystems, since under highly fertile conditions only a few species are able to compete successfully (Tilman 1982, Hautier et al. 2009). Today's grassland management faces a huge variety of ecological and societal requirements that have to be met by management practices. Management practices have to balance low N fertilization and high quality fodder production on the one hand, as well as ecosystem goods and services on the other hand. At the same time, the plant nutrient balance has to be considered, because from Liebig`s law of the minimum we know that only one nutrient in deficiency can be the limiting factor for biomass production. In general, increased plant resource use efficiency could be the key to balance economic needs and environmental benefits (Rockström et al. 2013).

The need to reduce synthetic nitrogen fertilization brings traditional and nearly forgotten land use practices back to light. Before the introduction of mineral fertilizers, flood irrigation used to be a common way for soil and yield improvement over large parts of temperate European grassland (Leibundgut & Kohn 2014, Schellberg 2005). Positive effects of irrigation such as increased biomass production, reduced herbivory, pest control and soil deacidification (Hassler 1995, Leibundgut 2014) are based on farmers' experiences. However, soil water availability can be seen as the mostly restricting factor for plant nutrient uptake and thus primary productivity during dry summer months (Kaye & Hart 1997). Irrigation thus might provide a way to counteract these losses in primary productivity as it may increase nutrient availability causing an indirect fertilization effect especially during drier periods (Leibundgut 2014, Stearne & Cook 2014) through the mobilization of exchangeable nutrients. Traditional meadow irrigation could therefore be a sustainable management practice that increases nutrient use efficiency, reduces nitrogen surplus and thus balances economic and environmental benefits (Müller et al. 2016b).

The most obvious trait related to nutrient use efficiency (NUE) is root architecture. Plants widely differ in their belowground strategies of taking up nutrients and reacting to temporal and spatial heterogeneity in nutrient availability (Bardgett et al. 2014). The cycles of flooding and draining under irrigation create small-scale hot spots and hot moments for nutrient availability (Mc Clain et al. 2002). These pulses of nutrient availability challenge the plants competitive abilities and may lead to higher plant species diversity (Müller et al. 2016a,b). From fertilization studies we know that only a few highly-productive species are able to compete at high rates of N fertilization by suppressing others (*sampling effect model*, Tilmann 1999 and citations therein, Hooper et al. 2005). The underlying mechanisms for that are still under debate, however, it is evident that plant species and plant trait characteristics shape soil properties and thus nutrient availability in their rhizosphere (van der Krift & Berendse 2001, Bardgett et al. 2014 and citations therein). Besides architectural traits different plant species host different metabolic root traits which influence microbial mineralization processes (van der Krift & Berendse 2001, Bardgett et al. 2014) and thus are likely to alter the competitive advantages of microbes within the rhizosphere (Moreau et al. 2015). Hence, the influence of short-term water pulses on the plant available nutrients as created by irrigation will depend on the interplay between plant species-specific traits (mainly root traits) and the competition between plants and microbes within the rhizosphere (Butterbach-Bahl et al. 2011). The relationship between plants and microorganisms is simultaneously mutualistic and competitive as plants provide labile organic substances while microorganisms make nutrients available to the plants through mineralization processes (Liu et al. 2016). Denitrifying microorganisms are the strongest competitors for nitrogen in the rhizosphere (Kaye & Hart 1997 and citations therein) as they reduce nitrate or nitrite to gaseous NO, N_2O, or N_2 (Bremner 1997). N_2O is an obligatory intermediate during denitrification but is released to the atmosphere depending on soil water content and N availability (Bouwman 1996, Davidson et al. 2000). Both soil parameters are influenced by irrigation which creates optimum conditions for denitrifiers and therefor a highly competitive situation in the rhizosphere. A more efficient N uptake by plants would reduce the substrate for denitrification processes. Thus, the N_2O emission rate could be used as a non-destructive tool to draw conclusions from the N use efficiency of plants.

In our study we aim to reveal the consequences of traditional flood irrigation for plant available nutrients in Central European grassland. We hypothesize that through artificial flooding nutrients being mainly cations are solved from the solid bounded phase (e.g. bounded to clay minerals) to soil solutions more than under regular drier summer conditions. Furthermore the organic substance that incorporates nutrients are degraded more rapidly than they would under summer dry conditions simply because soil microbes and invertebrates can function better under relatively wet conditions than very dry conditions (Austin et al. 2004 and citations therein). Assuming latter to be true, the increased concentration of plant nutrients after flooding should be sustainable (weeks) not only during a short peak. We hypothesize nutrients to be enhanced after irrigation and therefore supporting biomass production whereas the intensity of this effect will depend on the respective plant species' competitive abilities.

Effects were investigated in a controlled mesocosm experiment with three referential grassland species (*Centaurea jacea*, *Polygonum persicaria* and *Holcus lanatus*) and in a field observational study under *Holcus lanatus* in four differently managed hay meadows (non-irrigated/unfertilized, non-irrigated/fertilized, irrigated/unfertilized, irrigated/fertilized). N_2O emissions were used as a tool to measure N utilization efficiency where lower N_2O emissions indicate higher efficiency. Plant root simulators^{TM} were applied to measure plant available ions before, during and after the irrigation treatment.

In the mesocosms (1) we expected (1a) higher soil nutrient availability after irrigation whereas availability of redoxsensitive nutrients (NO_3^-, S, Fe, Mn) will be enhanced more than simply dilutable nutrients. We expected (1b) hot moments of N_2O release (three days after irrigation according to Mummey et al. 1994).

We hypothesized species-dependent alterations of the general pattern of nutrient availability before, during and after flooding as could be expected from the species-specific root architecture. *H. lanatus* as a representative of the grass species with their characteristic fibrous and dense root system was expected to be an efficient nutrient trap in the upper soil layers and thus having minor losses of nutrients suspicious to leaching (NO_3-N, Ca, Mg, Mn, B) after irrigation. In the long run, however, *H. lanatus* will decrease soil nutrient pools as a consequence of its higher biomass productivity to a larger extent than the two other species which will result in a lower nutrient availability before irrigation (long-term pattern). The high biomass productivity and accompanied efficient N use efficiency of *H. lanatus* will also reveal significant differences in the sensitive N_2O fluxes with lower emission rates under *H. lanatus* (less N available for soil microorganisms) compared to the other species. For all other measured matter (cations and anions) the variability will be too high to find clear pattern at the short term scale.

In the field study we hypothesize that all experimental findings will be confirmed at lower certainty because of less well controlled driving parameters. In detail this would be overall nutrient availability to be higher in fertilized meadows and a short-term higher nutrient availability in irrigated meadows irrespective of fertilization after irrigation. Further we expect a hot moment N_2O peak shortly after irrigation. In the non-irrigated meadows we assume nutrient availability to be decreased in the third measurement period, which is concurrent to the measurement after irrigation in irrigated meadows.

Material & Methods

Mesocosms: Species

We used *Holcus lanatus*, *Polygonum persicaria* and *Centaurea jacea* as reference species. The main distinctive functional characteristics between the chosen species are their root traits which are important drivers of ecosystem processes especially nutrient utilization efficiency (Bardgett et al. 2014). In a small-scale vegetation survey (1 x 1 m plot size) all three plant species benefited from irrigation and fertilization (Müller & Viedt, unpublished data).

H. lanatus forms an adventitious root system with numerous laterals which is characteristic for monocotyledon species. *P. persicaria* and *C. jacea* both have a primary roots system whereas *P. persicaria* has distinctive lateral branching and *C. jacea* produces a rather short taproot.

Further the selected species have distinctive clonal growth traits. *H. lanatus* builds runner shoots or ramets which undergo the natural life cycle. A population of these tillers forms one individual. *P. persicaria* is non-clonal not building any types of ramets and not spreading laterally. *C. jacea* spreads laterally through the growth of adventitious buds on adventitious roots. These clonal growth traits give them distinctive capabilities to for spatial as well as temporal utilization of nutrients. Clonal growth traits are important drivers of plant competitive success in heterogeneous environments and thus further are likely to impact biodiversity at a site (Eilts et al. 2013).

Species sampling and arrangement

Samples were taken from an irrigated unfertilized meadow close to Ottersheim (Germany, Rhineland-Palatinate, 32U 443900E 5451300N). The mean annual temperature of the region is 10.5 °C, with mean annual precipitation of 667 mm (station Landau; German Weather Service). Soil is loamy (41.8% clay, 23.9% sand, 34.1% silt with a pH of 5.4. The vegetation community belongs to the Arrhenaterion eliatoris alliance which is common for lowland mesophilic hay meadows.

Six undisturbed replicates were taken around an individual of the respective plant species directly from the field using a core cutter and fitted into an acrylic glass cylinder (55 cm in height, 30 cm diameter). Samples were taken down to 20 cm soil depth to cover the main part of the rhizosphere. The columns were closed at the bottom and immediately taken to the laboratory. The soil part of the pipe was wrapped with aluminium foil to shade the soil from the side as the pipes were transparent. Samples were exposed to four daylight imitating light bulbs (MT 250 DL Clean Ace, 250W, Eye European Lighting LTD). The mean room temperature over the measurement cycle was 21.3 °C. The treatments and measurements started one week after the sampling. Water for the irrigation experiment was taken from the adjacent river Queich and applied from above close to the soil surface to a water-level of 20 cm above the soil surface. The irrigation measurement was done 12 hrs after water application to avoid immediate disturbance effects. Afterwards the columns were drained slowly through the valves at the bottom.

Above- and belowground biomass

After the experiment we clipped the aboveground biomass in each mesocosm at ground-level. The sampled biomass was oven-dried at 72°C for 48 h to determine dry-weight biomass.
For belowground biomass the soil of the mesocosms was soaked for 30 minutes to break down soil aggregates. Afterwards the soil (including the belowground biomass) was sieved (2 mm diameter pore size) and any excess soil was washed of the roots. Biomass was oven-dried at 60°C for 48 h to determine the dry-weight.

Plant Root Simulators

Plant Root Simulators^{TM} (PRS; Western Agricultural Innovations, Saskatoon, Saskatchewan, Canada) are plastic sticks with integrated ion exchange resin membranes to measure plant available anions and cations directly in soil. Three probes for anions and three probes for cations were inserted into each mesocosm before (5 days), during (1 day) and after (5 days) the irrigation treatment. After retrieval adherent soil was washed of the PRS with deionized water. Analyses of the adsorbed ions were performed by Western Agricultural Innovations using colorimetry for NO_3-N and NH_4-N and inductively-coupled plasma spectrometry for the other ions (P, K, S, Ca, Mg, Al, Fe, Mn, Cu, Zn and B). The preparation and analysis processes are described in Hangs et al. 2004.

Mesocosm gas sampling

N_2O emissions were measured adopting the closed chamber method (Flessa et al. 1998). Measurements were done one day before irrigation, during irrigation (1 day) and over a period of 3 days after irrigation. Gas samples were collected in evacuated glas bottles (22.5 ml) with butyl-rubber septa.

Field measurements

Study sites

Study sites were selected according to their irrigation (yes/no) and fertilization (yes/no) status. Irrigated meadows are irrigated 2 times per year (spring and summer). Fertilized meadows receive 50-60 kg N^{-1} ha^{-1}. For each management type three meadows were selected. Soils of the investigated meadows are loamy to humus-rich sandy soils and one is a clayey loam soil. Soil pH values range from 4.9 to 6.9. Irrigated meadows are usually irrigated in April/May and August. The traditional flooding method in the region is to dam water of the river and let it stream into the meadows and back into the river through a system of open water channels. This leads to a relatively homogeneous water flow to prevent accumulation of stagnant water (Hassler et al. 1995, Leibundgut & Kohn 2014a). Each flooding event lasts 2-3 days (detailed description of the region is found in Müller et al. 2016a, b). The farmers did not need the second irrigation event in the year the study was carried out due to sufficient rainfalls during August. Therefor a controlled irrigation event was initiated for our field measurements in September after a period of dry weather.

H. lanatus was selected as test-species since it grows in all of the selected meadows and is controllable as it is possible to define and select one individual. Plastic soil rings were installed permanently around one individual of *H. lanatus* 4 weeks before the measurement period to prevent immediate disturbance effects.

Field Plant Root Simulators

PRS probes were installed within the soil ring in the rhizosphere of *H. lanatus*. The first (before irrigation) and the third measurement cycle (after irrigation) lasted for 21 days whereas the second measurement cycle (during irrigation) lasted 3 days. PRS probes were renewed between each measurement cycle immediately after the previous gas sampling to avoid disturbance effects. After measurement PRS probes were treated the same as in the mesocosm experiment.

Field gas sampling

Gas samplings were taken once a week for 9 weeks in total from August to September 2014 with the closed-chamber method (Flessa et al. 1998). Measurements were performed in the morning and within a short time-span for all meadows to avoid the influence of increasing temperatures on N_2O fluxes (Bremner & Blackmer 1980).

Data Analysis

Data analysis procedures were the same for mesocosm and field data. The analysis procedures were carried out with the statistical program R 3.1.2 (R Core Team 2014) using the package vegan (Oksanen et al. 2015) and MASS (Venables & Ripley 2002).

PRS data for the different nutrients were averaged over all three species to evaluate the general pattern of nutrient availability before, during and after irrigation. For the evaluation of the species effect on nutrient availability nutrients data of the three species was treated separately. Statistical significance of the differences between the three time points (before, during and after irrigation) for the general nutrient availability as well as the species-dependent nutrient availability were tested with ANOVA with a subsequent Tukey post-hoc test, if the assumption of homogeneity of variances was not violated (Levene's test from means). If homogeneity of variances was not given Friedman test with a subsequent Wilcoxon pairwise test was performed. Assumption of normality was checked using Shapiro-Wilk test. If tests assumptions were violated data was log-transformed. Differences in the group means of N_2O emissions for the three regarded species were tested with t-tests. The relationship between total biomass (sum of aboveground and belowground biomass) and N_2O emissions for each day was tested with linear regression.

Results

Mesocosms

General nutrient availability before, during and after irrigation

Regarding their availability after irrigation nutrients can be assigned to three groups (Fig 1):

1. NO_3 was the only nutrient that had a significantly higher availability after irrigation.
2. Most nutrients were less available after irrigation than before irrigation. Nutrient availability was significantly lower after irrigation for NH_4, P, Ca, S, Mg, Fe, Mn, Cu, Zn and non-significantly lower for B.
3. K reacted indifferently to irrigation.

During irrigation nutrient availability peaked for all nutrients except for K and P (Fig. 1) even though it represents only 1 day of measurement. The comparison of redoxsensitive (NO_3, S, Mn, Fe) and non-sensitive nutrients (NH_4, P, K, Ca, Mg, Cu, Zn, B) revealed a significantly higher increase (781% vs. 123% increase, $p = 0.039$) in the availability of redoxsensitive nutrients during irrigation.

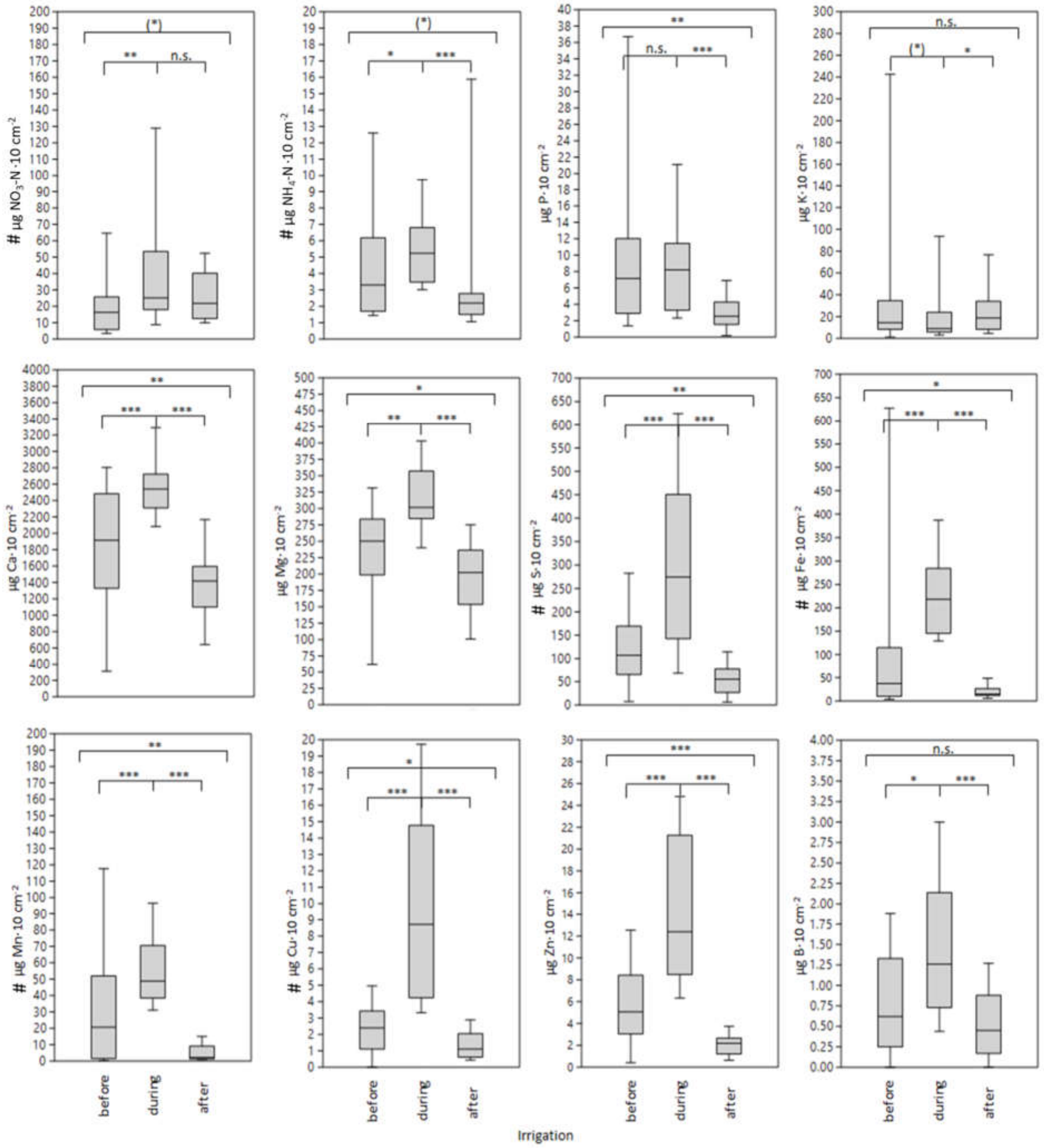

Fig. 1. Mean plant available nutrients (Plant Root Simulators) before, during and after irrigation. Nutrient availability before and after irrigation was measured for 5 days whereas nutrient availability was measured for one day. Significant differences between the measurement periods were tested with pairwise t-tests. Data was log-transformed if the assumption of normality was violated. n.s. $p > 0.1$, (*) $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Species-specific nutrient availability

Differences in rhizosphere nutrient availability before irrigation

In general *H. lanatus* had the overall lowest availability of all nutrients except for K before irrigation whereas nutrient availability was highest for all nutrients except for K and S under *P. persicaria*. Comparing the three species among each other we found significant differences in their rhizosphere nutrient availability before the irrigation event (Fig. 2):

Ca, Mg, Mn, Zn and B were significantly lower in mesocosms planted with *H. lanatus* compared to *P. persicaria* and *C. jacea* whereas Fe and Cu availability was only significantly lower under *P. persicaria*. Only K availability was significantly higher under *H. lanatus* than under the two other species before irrigation. *P. persicaria* showed a significantly higher availability of Fe and Cu than the two other species. Ca, Mg, Zn, B, were significantly higher under *P. persicaria* than under *C. jacea*.

Impact of irrigation on the rhizosphere nutrient-availability

Centaurea jacea basically followed the same pattern as the general pattern of nutrient availability. (Fig. 2 and Table 1). NO_3 and K availability increased after irrigation. For all other macronutrients and all micronutrient except B (insignificant increase) availability was lower after irrigation. During irrigation the availability of NO_3, NH_4, P, Ca, Mg and S was higher than before irrigation.

Polygonum persicaria showed a decrease in the availability of all macro- and micronutrients after irrigation. The decrease was significant for NH4, P (marginal), Ca, Mg, Fe, Mn, Cu, Zn, B. Furthermore during the one day of irrigation NH_4, P and K were also less available whereas NO_3, Ca, Mg, S increased in their availability.

Holcus lanatus revealed a different pattern than the other two species. NO_3, NH_4, Ca, Mg and S availability was increased after irrigation. We only found a decrease for K and S. For P the availability after irrigation remained similar to the availability before irrigation. On behalf of the micronutrients we found a marginally significant increase in Fe availability after irrigation whereas the other micronutrients remained fairly stable. During irrigation all macronutrients except K peaked under *H. lanatus*.

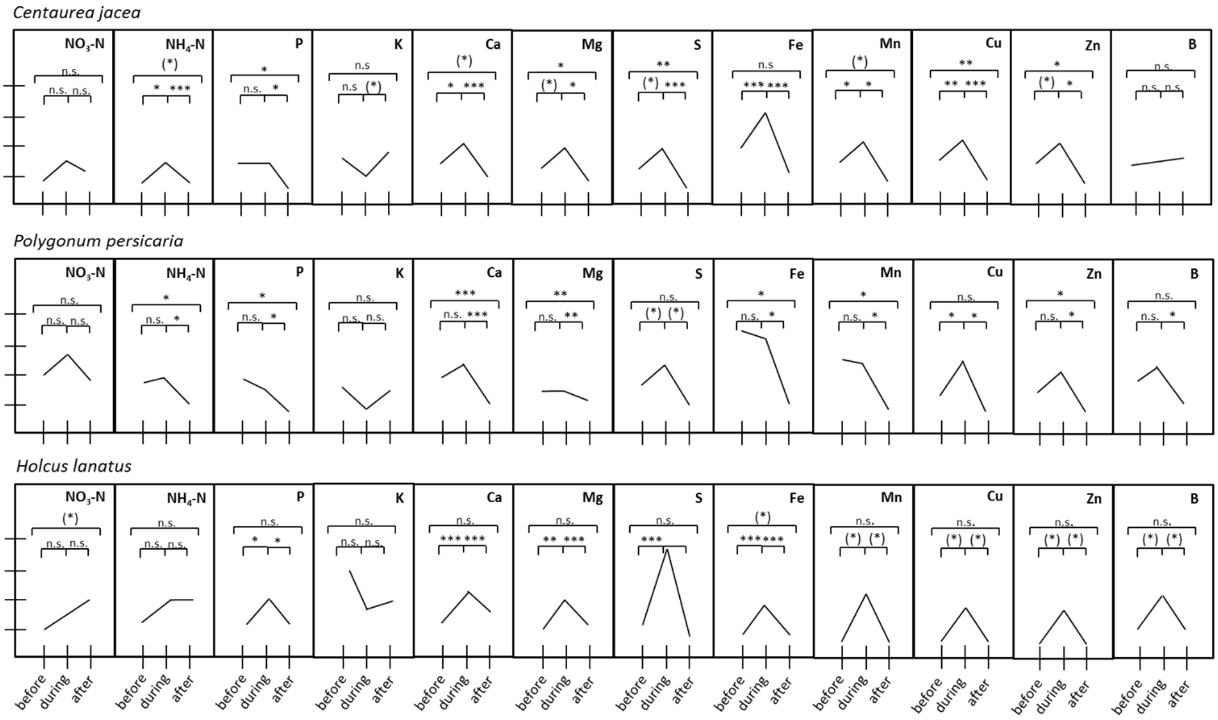

Fig. 2. Schematic graph of nutrient availability before, during and after irrigation in mesocosms planted with three functionally distinct grassland species. n.s. $p > 0.1$, (*) $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

General N_2O emission rates

The N_2O emission rates followed the expected pattern which means emissions were lowest during irrigation and constantly increased afterwards (Fig. 3). Three days after irrigation peaks were measured for all mesocosms as predicted. Variances were high before irrigation and three days after irrigation. Variance was low during irrigation (low diffusion rate). Fluxes before and during irrigation as well as fluxes before and three days after irrigation were significantly different from each other.

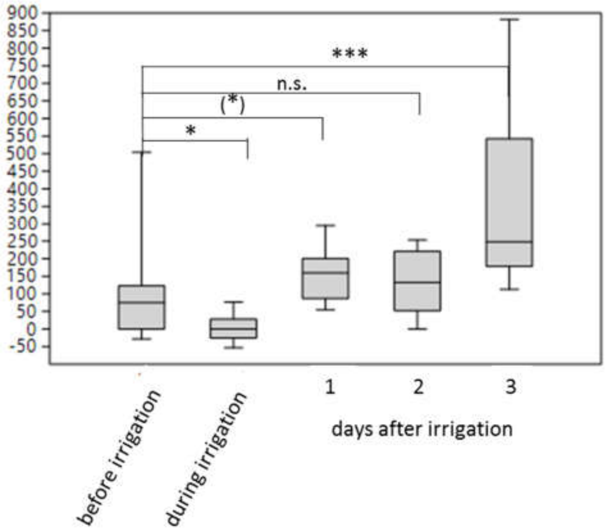

Fig. 3. N_2O emissions over all mesocosms irrespective of the regarded species before, during and three days after irrigation. . n.s. $p > 0.1$, (*) $p < 0.1$, * $p < 0.05$, $p < 0.01$, *** $p < 0.001$.

Species-specific N_2O emission rates

Basically the same pattern was found as for the daily fluxes irrespective of the species (Fig. 4). Exceptions are: Day 1 (before Irrigation): *P. persicaria* had significantly higher emission rates than the other two species. Day 5: *H. lanatus* showed the lowest emission rates. This pattern is also confirmed in the cumulative emissions of the three days after irrigation and so *H. lanatus* emitted the lowest amount of N_2O (Fig. 4).

Before irrigation mean N_2O emission rates were significantly lower in mesocosms with *H. lanatus* compared to mesocosms with *C. jacea* ($t = 2.485$, $p = 0.037$) or *P. persicaria* ($t = 2.522$, $p = 0.032$) respectively. The variances were significantly larger in *C. jacea* than in *P.*

persicaria (F = 7.607, p = 0.071) as well as in *P. persicaria* than in *H. lanatus* (F = 22.958, p = 0.009).

During irrigation emissions were low (near zero) to negative in all mesocosms. Three days after irrigation emissions were significantly lower in mesocosms with *H. lanatus* compared to *P. persicaria* (t = 2.477, p = 0.035) whereas N_2O emissions from mesocosms with *P. persicaria* and *C. jacea* did not differ significantly (Fig. 4). Variance of N_2O flux rate was significantly higher in mesocosms with *H. lanatus* compared to *C. jacea* (F = 24.663, p = 0.008) and *P. persicaria* (F = 18.506, p = 0.014). Flux rates in mesocosms with *H. lanatus* increased one day after irrigation and decreased three days after irrigation (Fig. 4). For *C. jacea* and *P. persicaria* the N_2O flux rates increased from the first day after drainage and resulted in the peak three days after irrigation. The cumulative emissions for the three days after irrigation (sum) revealed the lowest mean emission rates for *H. lanatus* and the highest mean emission rates for *P. persicaria* (Fig. 4). However the differences in the mean emission rates as well as the variances were not significant.

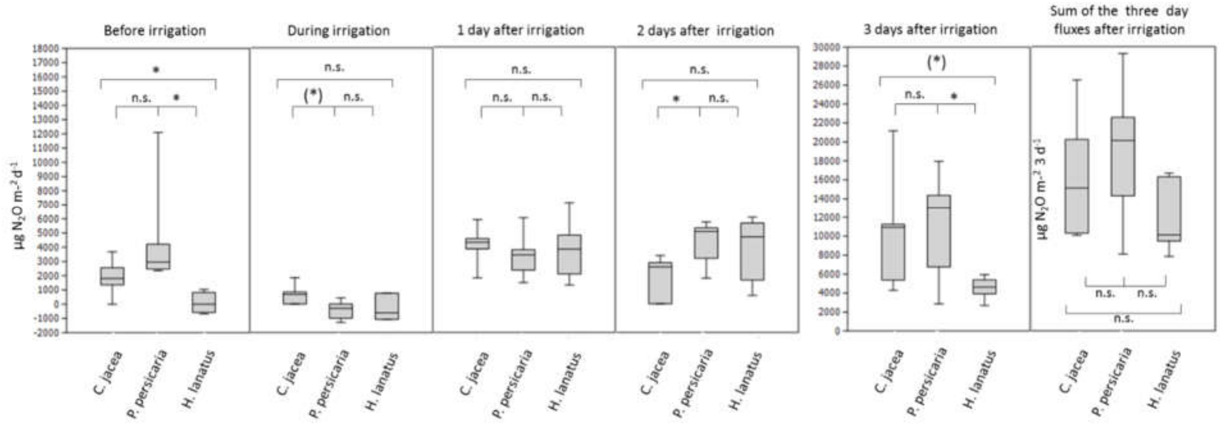

Fig. 4. N_2O flux rate from soils cultivated with three different species in mesocosms before, during and three days after irrigation. . n.s. $p > 0.1$, (*) $p < 0.1$, * $p < 0.05$.

Biomass

H. lanatus had approximately 1.5 times more above- (9.2 ± 5.0 g) and belowground biomass (55.9 ± 0.6 g) compared to *P. persicaria* (34.6 ± 4.6) and *C. jacea* (37.2 ± 6.9) at the end of the experiment (Fig. 5). All plants had roughly 5 times more belowground than aboveground biomass (Fig. 5). Below- and aboveground biomass are only slightly positively correlated (Pearson correlation = 0.40).

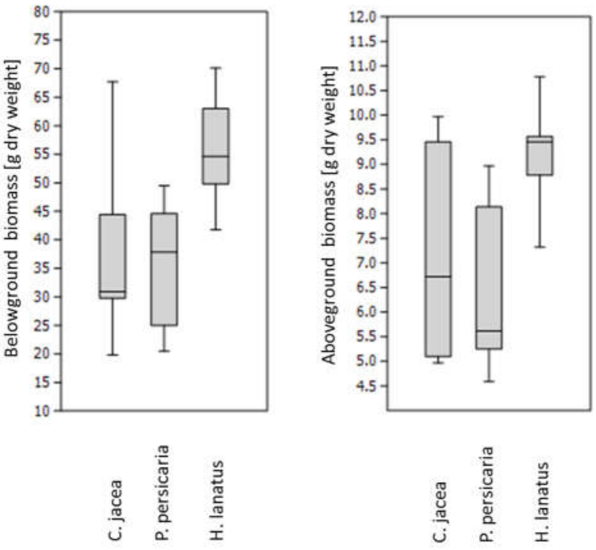

Fig. 5. Above- and belowground dry weight biomass of the three investigated species.

Above- and belowground biomass apparently had a significantly negative influence on N_2O emissions as peak height decreased with increasing biomass before irrigation ($r^2 = 0.351$, $t = 2.656$, $p = 0.024$). This effect was diminished during irrigation until two days after irrigation (no significant correlation) and appeared again marginally significant three days after irrigation ($r^2 = 0.174$, $t = 1.779$, $p = 0.097$).

Field measurements

Nutrient availability under H. lanatus in differently managed meadows

The patterns found in the field measurements confirmed the experimental insights found in the experimental setup. A major exception is the fact that irrigation did not lead to higher NO_3 availability after irrigation on the fertilized meadows

(Tab. 1). Further, N supply by nitrate was clearly lower, which was even true for the fertilized sites.

Before irrigation some meadows revealed distinctive nutrient availabilities depending on management:

- NO_3 availability was significantly higher in irrigated/fertilized meadows than in unfertilized meadows irrespective of irrigation but it was significantly higher in irrigated/unfertilized than in non-irrigated meadows without fertilization.

- Mg availability was higher in non-irrigated and fertilized meadows compared to irrigated and fertilized meadows.
- Cu availability was higher in irrigated/unfertilized than in non-irrigated/fertilized meadows and also higher in irrigated/fertilized than in non-irrigated/fertilized meadows.
- Zn availability was higher in irrigated/unfertilized than non-irrigated/unfertilized meadows. Zn availability was also higher in irrigated/unfertilized than non-irrigated/ fertilized meadows.

During the three measurement periods availability of all nutrients decreased or remained stable. In contrast to that availability of NH_4, Ca, S, Fe, Mn, Cu and Zn increased significantly after irrigation in traditionally irrigated meadows. This increase was independent whether the meadows were fertilized or not. Only in irrigated and unfertilized meadows an increase in NO_3 was detected. Both irrigated meadows with and without fertilization decreased in their K availability after irrigation whereas irrigated and fertilized meadows also decreased in their P availability which remained relatively stable (> 1 $\mu g \cdot 10\ cm^{-2}$ * 20 days decrease) in irrigated and unfertilized meadows. Irrigated and unfertilized meadows also lost NH_4 after irrigation whereas B availability was indifferent (> 1 $\mu g \cdot 10\ cm^{-2}$ * 20 days decrease).

Tab. 1. Plant available nutrients (mean and SE) under *H. lanatus* in irrigated and non-irrigated meadows with and without fertilization. Nutrient availability before and after irrigation was measured for 5 days and during irrigation for 1 day. Data in bold indicate statistical significance ($p \leq 0.05$) and bold italics indicate marginal significance ($p \leq 0.1$) between the three measurement periods. Statistical significance was only tested for nutrient availability before versus after irrigation.

Macronutrients (µg nutrient*10 cm² ion exchange membrane)

Site	**Irrigation**	**NO_3-N**	**NH_4-N**	**P**	**K**	**Ca**	**Mg**	**S**
				Unfertilized				
Irrigated (a)	Before (20 days)	**5.4 ± 1.47**	**2.89 ± 0.2**	4.38 ± 0.92	**26.96 ± 5.26**	**2245.56 ± 112.58**	286.74 ± 11.31	**81.65 ± 13.51**
	During (1 day)	7.42 ± 1.71	6.85 ± 0.67	2.9 ± 0.81	23.57 ± 3.7	1826.41 ± 65.99	262.69 ± 12.4	467.18 ± 61.79
	After (20 days)	**8.51 ± 2.25**	**4.34 ± 0.46**	4.01 ± 1.26	**16.72 ± 4.29**	**2656.57 ± 83.24**	284.31 ± 12.37	**189.58 ± 12.52**
Non-irrigated (b)	1 (20 days)	3.99 ± 0.27	3.07 ± 0.15	**8.35 ± 1.08**	14.96 ± 2.46	**1906.12 ± 129.05**	**289.35 ± 24.47**	**91.64 ± 13.89**
	2 (1 day)	2.57 ± 0.13	2.78 ± 0.36	1.18 ± 0.18	10.79 ± 1.8	277.84 ± 18.57	51.68 ± 3.76	14.99 ± 1.25
	3 (20 days)	5.41 ± 1.34	3.49 ± 0.71	**4.39 ± 0.99**	31.14 ± 9.4	**1256.89 ± 94.92**	**200.3 ± 16.09**	**55.02 ± 7.94**
				Fertilized				
Irrigated (c)	Before (20 days)	9.57 ± 2.46	**3.73 ± 0.48**	***9,39 ± 3.22***	***29.33 ± 9.7***	**1867.19 ± 104.77**	236.61 ± 11.81	**13.05 ± 3.06**
	During (1 day)	3.47 ± 0.54	7.44 ± 1.13	2.61 ± 0.68	21.58 ± 5.03	1086.68 ± 161.13	158.81 ± 22.15	69.77 ± 20.16
	After (20 days)	8.2 ± 2.4	**5.18 ± 0.43**	***5.20 ± 2.42***	***8.23 ± 1.23***	**2175.27 ± 62.6**	245.43 ± 8.76	**125.86 ± 37.63**
Non-irrigated (d)	1 (20 days)	4.44 ± 0.54	2.91 ± 0.24	**15.29 ± 5.85**	36.4 ± 13.12	**2070.35 ± 113.66**	**319.98 ± 13.31**	**65.06 ± 5.78**
	2 (1 day)	5.08 ± 0.88	13.71 ± 6.96	3.29 ± 1.10	22.06 ± 5.1	517.26 ± 50.3	90.99 ± 7.31	19.9 ± 2.44
	3 (20 days)	9.28 ± 2.36	2.85 ± 0.23	**8.79 ± 3.81**	38.49 ± 12.99	**1445.54 ± 129.64**	**217.13 ± 16.65**	**32.87 ± 4.95**

Micronutrients (µg nutrient*10 cm^2 ion exchange membrane)

Site	**Irrigation**	**Fe**	**Mn**	**Cu**	**Zn**	**B**
Unfertilized						
Irrigated (a)	Before (20 days)	**8.58 ± 1.51**	**1.2 ± 0.12**	**2.44 ± 0.45**	**4.85 ± 0.78**	0.58 ± 0.09
	During (1 day)	57.11 ± 6.98	43.68 ± 7.16	3.38 ± 0.72	6.88 ± 1.19	1.08 ± 0.28
	After (20 days)	**92.28 ± 15.48**	**21.56 ± 6.42**	**9.74 ± 1.47**	**11.36 ± 1.4**	0.71 ± 0.11
Non-irrigated (b)	1 (20 days)	**7.13 ± 2.14**	**1.46 ± 0.39**	**1.09 ± 0.44**	**1.9 ± 0.68**	0.81 ± 0.12
	2 (1 day)	1.82 ± 0.24	0.32 ± 0.08	n.a.	0.44 ± 0.07	0.58 ± 0.08
	3 (20 days)	**2.6 ± 0.41**	**0.59 ± 0.12**	**0.39 ± 0.05**	**1.07 ± 0.27**	0.61 ± 0.09
Fertilized						
Irrigated (c)	Before (20 days)	**13.05 ± 3.06**	**1.55 ± 0.3**	**2.26 ± 0.76**	**4.11 ± 1.16**	0.38 ± 0.1
	During (1 day)	69.77 ± 20.16	59.01 ± 10.41	0.88 ± 0.13	2.15 ± 0.31	0.77 ± 0.1
	After (20 days)	**125.86 ± 37.63**	**20 ± 4.33**	**4.59 ± 0.79**	**6.1 ± 1.29**	0.7 ± 0.12
Non-irrigated (d)	1 (20 days)	***5.53*** **±** ***0.64***	**1.57 ± 0.24**	0.27 ± 0.01	1.31 ± 0.1	**0.87 ± 0.24**
	2 (1 day)	2.54 ± 0.23	0.44 ± 0.08	n.a.	0.37 ± 0.06	0.87 ± 0.17
	3 (20 days)	***3.96*** **±** ***0.38***	**0.68 ± 0.09**	0.41 ± 0.14	1.07 ± 0.12	**0.41 ± 0.11**

N_2O fluxes under H. lanatus in differently managed meadows

Mean N_2O fluxes ranged from -5 to 16 µg N_2O m^{-2} h^{-1}. The highest range (-3 to 16 µg N_2O m^{-2} h^{-1}) was found for irrigated and unfertilized fields. The ranges are close to detection limits. Peaks could not be detected for neither of the management types.

Discussion

Our results basically support the experience of centuries that traditional flood irrigation of meadows has the potential to partly subsidize fertilization. However, it is not a straight forward feedback loop. During the day of flooding nearly all nutrients had a higher availability, however, this was not as enduring as expected. For all nutrients but NO_3 the availability was even reduced after flooding compared to before flooding. Hence we have the pattern of medium availability (10 days before the flooding), highest availability (at the day of the flooding) to lowest availability (10 days after flooding). Therefore we truly have a hot moment of nutrient availability since availability of nearly all nutrients (except K) during one day of irrigation exceeded the availability during the 10 days before and after irrigation. This pattern could either be the result of the efficient uptake of nutrients during the nutrient peak or the loss nutrients through leaching during drainage. A loss of nutrients through percolation from the upper soil part to lower soil horizons is possible and needs to be assumed (Cook et al. 2015). NO_3 as the preferential N form for plants increased in its availability after irrigation which could be a result of its high mobility in soil solution which facilitates the transport to the root surface (Owen et al. 2001, Liu et al. 2016). Leonardson et al. (1994) found plants to assimilate more N in irrigated meadows than in non-irrigated meadows exhibiting the advantages of irrigation for plant N utilization. Besides N, P and K belong to the three most abundantly applied elements (NPK fertilizers). P fertilization is most recently discussed as an even greater threat on grassland biodiversity than N (Ceulemans et al. 2013, Ceulemans et al. 2014). During irrigation P did not exhibit a considerable peak such as most of the other nutrients did but there was a clear loss after irrigation. P from agricultural and sewage discharges (depending on the adjacent environment) could be transported into the meadow with the irrigation water but is likely to be trapped as the water flows through the meadow and thus being diminished from the stream across the meadow (Cook et al. 2015). However, the bulk of P is fixed in chemical complexes (organic matter, Fe, Al, Ca) and is not available for the plants even during the irrigation (Cook et al. 2015). On the other hand, K is reacting contrary to nearly all other elements. The lower K content during irrigation is due to the shorter (1 day versus 5 days) measurement period and the inexistent peak in contrast to most of the other nutrients.

The strong increase in the availability of redox-sensitive nutrients during only one day of submersion gives reason to assume fast oxygen depletion. Presumably anoxic or at least hypoxic conditions where reached in the upper rhizosphere in less than one day of flooding. This fast reaction is advantageous for manganese as Mn-oxides are reduced to plant-available Mn_2^+. Irrigation in our mesocosms doubled Mn availability during the flooding period compared to the availability before irrigation although it represents only one day. Comparable high increases during irrigation were also found for Fe, Cu and S. The pattern found for Mn was very similar to the Fe-pattern under all three species. The Cu peak during irrigation is likely to be a result of the increasing redox potentials in the flooded soils (Schulz-Zunkel 2013). Sulfur deficiency has become a major threat to plant productivity within the past decades (Lewandowska & Sirko 2008) but irrigation did not improve S supply sustainably. Thus it depends on the plant's ability to use the S peak during irrigation. Soil water and consequential nutrient pulses as created by irrigation are likely to set off the balance between nutrient mineralization and immobilization by stimulating microbial mineralization rates and could thus be crucial drivers of plant productivity (Leonardson 1994, Cook et al. 2003, Austin et al. 2004). However the nutrient peak was not as sustainable as expected which became obvious even at the short-term scale of three days after irrigation. Thus a total abandonment of fertilization is not possible as the biomass and therefor the bulk of nutrients becomes regularly removed in hay meadows which would lead to severe nutrient impoverishment in the long run. A precise adjustment of fertilization and irrigation could still help to improve fertilizer nutrient utilization and prevent high losses and as follows reduce the need of overfertilization. Irrigation could therefore be a way to overcome deficiencies through drought stress during critical growth stages, improve nutrient utilization and as follows elevated biomass production with reduced N fertilization.

Of all measured nutrients only NO_3 exhibited an enhanced availability beyond the irrigation (3 days) and apparently this was even restricted to *H. lanatus*. At the same time less N_2O was emitted from the *H. lantus* – soil systems than did from the other two plant-soil systems. This is a clear hint that species-specific traits matter and *H. lanatus* is capable of utilizing the surplus of NO_3 because usually a surplus of nitrate will be used by microorganisms resulting in enhanced N_2O emissions (Liu et al. 2016). In contrast to *H. lanatus*, the distribution of the N_2O flux rates under *C. jacea* and *P. persicaria* with relatively low rates before irrigation, zero to negative fluxes during complete inundation and a peak of N_2O within 60 h after drainage are representative for irrigation treatments (Mummey et al. 1994). Biomass seemed to be decisive for N_2O emission rates as they decreased with increasing biomass (*P. persicaria* > *C. jacea* > *H. lanatus*). *P. persicaria* can thus be expected to be least efficient in taking up the available N during and shortly after irrigation. This is also supported by the lower variance in N_2O emission rates under *H. lanatus* than *C. jacea* and *P. persicaria* three days after irrigation which indicates a faster re-establishment of the original balance in mesocosms with *H. lanatus*. The distinct pattern of nutrient availability under *H. lanatus* during the three measurement periods go along with its shallow dense root architecture which allows to access a wider area of the upper soil layers and explaining its incomparable higher belowground biomass. Such dense root systems reduce N leaching from soil, enhance N cycling and the hydraulic lift of water in the surface soil (Bardgett et al. 2014 and citations therein). It is likely that the functional advantages of *H. lanatus* are also beneficial for the uptake of other nutrients available in the upper soil layers as well as the exploitation of water-driven nutrients explaining the decreased nutrient losses under *H. lanatus* after irrigation. The distinct pattern of nutrient availability before irrigation reflects the long-term nutrient utilization efficiency as we can act on the assumption that plant species shape their rhizosphere environment (van der Krift & Berendse 2001, Bardgett et al. 2014 and citations therein). As *H. lanatus* mesocosms started with a considerably lower nutrient availability for almost all nutrients except K it can be assumed that *H. lanatus* is even more efficient than the two other species in the long run. The clonal growth of *C. jacea* enables the plant to cope with heterogeneous nutrient distribution at the field scale (Hutchings & de Kroon 1994, Eilts et al. 2013) and rapidly capture resources (Moora et al. 2004) which makes the species a competitive strategist (Grime 2001). However, this ecological advantage is restrained in our mesocosms due to the spatial restriction. Nevertheless mesocosms with *C. jacea* followed the general pattern and seemed to be more advantageous than *P. persicaria* for the availability of at least some nutrients during irrigation since there were more concise peaks for Mg, Fe, Mn and lower losses for NO_3, NH_4, Ca, Fe, Mn, B after irrigation. *C. jacea* even slightly profited from irrigation in the long run regarding the NO_3-availability. For P only *H. lanatus* exhibited a clear peak during irrigation as well as negligible losses after drainage. This fortifies the assumption that grass species act as nutrient traps (Cook et al. 2015) which may be ascribed to their fine branched root architecture. Thus grass species are likely to benefit highly from the nutrient peak in irrigated meadows. Their functional advantage to capture resources efficiently is also manifested in their high biomass gain under intensive N and P fertilization. Anyway irrigation does not foster a clear dominance of grass species and is beneficial for plant species richness (Müller et al. 2016) which confirms the assumption that plant species benefit differently from irrigation depending on their functional traits affecting their nutrient utilization efficiency.

In the field the pattern of increased nutrient and specifically N availability during and after irrigation were less distinct due to an overall lower nutrient availability but still availability of NO_3, NH_4, Ca, S, Fe, Mn, Cu and Zn was increased after irrigation. Thus field measurements supported the findings from the experimental setup to a certain degree so that we can act on the assumption that irrigation fosters plant nutrient availability on a short-term scale. Drainage of the irrigation water is slower at the field site which may help to prevent high losses through leaching and may also keep the hot moment of nutrient availability up for more than one day. This appears meaningful, as elements are lost by the systems through biomass extraction (harvest/yield). The short irrigation cycles in our meadows with the constantly flowing water is unlikely to cause anoxic conditions in the topsoil (Cook et al. 2015) which may explain the low emission rates and the missing peak in the field experiment. The higher overall nutrient availability in the mesocosms compared to the field measurements even before irrigation could be due to aggregate destruction during the sampling process which may have led to a release of nutrients.

Conclusions

The combined investigation of irrigation in a controlled mesocosm experiment and in a field study under different management regimes revealed significant consequences of traditional flood irrigation on plant nutrient availability:

1. Irrigation creates a hot moment for the availability of essential macro- and micronutrients and potentially counteracts deficiencies whereas redoxsensitive nutrients showed the highest increase.
2. Irrigation can be fairly long-term beneficial only for NO_3 availability but not for other nutrients.
3. The degree of the beneficial effect of irrigation on plant nutrient availability is to a certain degree dependent on the plant species (rhizosphere effects) with *H. lanatus* as the most efficient nutrient trap.
4. The dry-wet-dry cycles caused by irrigation cause a N_2O peak three days after drainage.

5. The N_2O emission rate depends on the plant species nutrient utilization efficiency with highly productive species (high above- and belowground biomass) accounting for partially lower emission rates which is particularly true for the relation to available NO_3.
6. The patterns found in the mesocosms are less distinct at the field scale but nevertheless support the short-term beneficial effect of irrigation.

Irrigation could thus be a way to overcome water deficiency in summer and associated nutrient stress during critical growth stages and thus possibly enhance the efficiency of fertilization. The found effects are likely to vary depending on abiotic conditions (soil type, climate) which underlines the importance of a regional evaluation of the ecological and economical value of irrigation. From the point of view of plant biodiversity highly productive and widely dominant species such as *H. lanatus* could profit most from irrigation influencing the plant species composition substantially which is likely to depend on the fine coordination of fertilization and irrigation. However the distinct clonal growth of *C. jacea* could generate different effects at the field scale. Thus irrigation and fertilization must be balanced ecologically worthwhile to avoid detrimental effects on plant biodiversity. However plant uptake efficiency of other nutrients than N during and after irrigation needs further investigation

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Supporting information to the paper

Appendix D

D. 1. Nutrient availability in mesocosms under three grassland species**.**

D. 2. Results of the statistical analysis of the nutrient availability (general and species-dependent) in the mesocosms.

CHAPTER 6

SYNTHESIS

Isabell B. Müller

The present study investigated the impact of traditional flood irrigation on the biodiversity and nutrient cycling in Central European hay meadows. The interrelation between irrigation and fertilization was investigated regarding their long-term impact on the plant species diversity and plant functional composition as well as the invertebrate diversity. Based on the results from the species inventories, a combined field and laboratory experiment was developed to investigate the ecosystem processes, concerning plant nutrient availability and nitrogen utilization efficiency.

Intensive management and abandonment has pushed grassland biodiversity beyond its boundaries (Newbold et al. 2016) and consequently affects ecosystem multifunctionality (Hector & Bagchi 2007, Isbell et al. 2011, Allan et al. 2015). However, requirements on grassland management are manifold, reaching from the agricultural need of productivity, over the ecological need of biodiversity conservation, up to the socioecological need of an aesthetic flower-rich appearance. This bucket full of requirements makes trade-offs inevitable (Allan et al. 2015 and citations therein). Traditional extensive grassland management fosters biodiversity, but has become widely unprofitable in the light of economic requirements of grassland management (Strijker 2005). However, the globally decreasing grassland biodiversity due to intensification and abandonment attract notice to traditional management options such as traditional meadow irrigation. Traditional flood irrigation changes both the plant species and functional community and biodiversity on the long-term scale. The result of these changes are plant species communities with a higher diversity and a more even species abundance. Interestingly, the effects of irrigation on alpha- and beta-diversity were less pronounced in the first year of our study. This suggests the importance of long-term studies and raises the assumption that other abiotic factors such as weather conditions are likely to interact with the effects of irrigation (Herben et al. 1995, Andrey et al. 2014). The changes in the species community both on the functional as well as on the diversity level go along with other species inventories from flood irrigated meadows, which revealed species community changes after the abandonment of irrigation management (Hassler 1995 and citations therein). Traditional irrigation systems are historically adapted to regional landscape conditions, fostering landscape heterogeneity and thus plant diversity at the landscape level (β-diversity). A rather modern irrigation technique is sprinkler-irrigation, which applies the irrigation water as drip irrigation from above. A recent study by Riedener et al. (2013) investigated plant and arthropod community shifts in traditionally flood irrigated and sprinkler-irrigated meadows. However, both irrigation systems did not affect biodiversity negatively. Thus, a change in the irrigation technique itself does not cause biotic homogenization. Still, the effects of irrigation interact with other management factors such as fertilization intensity. Other factors such as grazing intensity, irrigation frequency and mowing intensity are also likely to interact with irrigation or even interfere with the positive effects of irrigation (Gaujour et al. 2012, Riedener et al. 2013). Species richness-water uptake patterns are temporarily distinguished, which can be ascribed to meteorological conditions (Leimer et al. 2014), explaining the less pronounced effects of irrigation during the first year of the study.

The short-term water pulses in irrigated meadows represent a form of disturbance that impacts nutrient cycling and mineralization processes (Leonardson et al. 1994) especially during drier periods of the year. Irrigation creates a hot moment of nutrient availability during submersion. The hot moment of nutrient availability created by irrigation can only be kept up for NO_3 for a few days after irrigation. Thus, irrigation alone may lead to nutrient loss in the long run if fertilization becomes completely substituted as most nutrients are lost through biomass extraction (Oehlmann 2007). Therefore, irrigation without additional fertilization cannot be sustainable for meadow management to fulfill the agronomic demands. It is likely that the nutrient pulses induced by irrigation affect the competitive structure within the plant species community as well between plants and soil microbiota (Liu et al. 2016). Plants hosting distinct traits (either below- or aboveground) will benefit differently from the shortly enhanced nutrient availability which supports plant community shifts (Spehn et al. 2005, Fornara & Tilman 2008). In turn, plant functional composition is a strong determinant of nutrient availability and thus creates a direct feedback loop on biogeochemical cycling (Hooper & Vitousek 1998, Scherer-Lorenzen et al. 2003, Tilman et al. 1997). Thus, the functional shifts within irrigated meadows are likely to be a result of the alterations in nutrient availability (spatially and temporarily) but also a determinant of distinct patterns of nutrient availability and nutrient uptake. NO_3 is the main N source for plants and the mostly limiting resource in terrestrial ecosystems (Vitousek et al. 2002). Thus competition for NO_3 determines the competitive structure within a community. The NO_3 peak after irrigation was mainly determined by *H. lanatus*. This seems plausible as grass species with their distint dense root system are able to buffer possible NO_3 leaching as they prevent the downflow of water, which is a major cause of NO_3 leaching (Hooper & Vitousek 1998, Leimer et al. 2014, Leimer et al. 2015). *H. lanatus,* as a representative of grass species, benefitted highly from the effect of irrigation on nutrient availability in our mesocosm experiment, which can be attributed to its high root biomass. Nevertheless, *H. lanatus* or other grass species were not dominant in irrigated meadows, which would be expected from these advantages during irrigation. In fact legumes benefitted substantially from irrigation. High legume abundance is actually an indicator of low nitrogen availability (Fornara & Tilman 2008) which arouses the suspicion that the nitrogen pulse during irrigation is not sufficient enough. However, it is most likely that legume species predominantely profit from the surplus water after irrigation since the effect was disentangled from fertilization and Riedener et al. (2013) could not detect a change in legume abundance between sprinkler and traditionally flood irrigated meadows. High legume abundance is not only an indicator of low N availability, but also exhibits directly influence on nitrogen (N) cycling in soil due the legume's N-fixation ability. This influence of legumes on soil fertility and the competitive structure of plant communities is widely studied (Spehn et al. 2002, Temperton et al. 2007, Gubsch et. al. 2011, Lüscher et al. 2014). The occurance of such highly complementary functional groups within a community and the high plant diversity support the assumption that complementarity effects through niche differentiation buffer the functional advantages of grass species during irrigation at the field scale, maintaining the balance in the species community (Tilman et al. 1996; Spehn et al. 2000, Loreau et al. 2001). This balance in the dominance patterns of the species community is further expressed in the higher structural complexity found in irrigated meadows. Research in sprinkler-irrigated Alpine mountain meadows also revealed a higher structural complexity of the vegetation in irrigated meadows, which was measured based on an improved Shannon Index (Andrey et al. 2014). The functional analysis of our species inventory based on growth types, separating species groups from different vegetative layers, exposed a possible explanation for the higher structural complexity. Usually, plants with a more basal leaf distribution are favored by grazing and early mowing, however, both management factors did not differ substantially between our meadows. Thus, irrigation seems to be the distinctive factor for the establishment of the high structural complexity. Structurally more complex grassland such as the irrigated meadows would be expected to offer more microhabitats for invertebrates and thus harboring a higher invertebrate diversity than non-irrigated meadows (Woodcock & Pywell 2010, Dittrich & Helden 2012). However, the effects of irrigation on biodiversity were less profound for invertebrate species although irrigation caused a shift in the community composition, favoring moisture-depended species. The beneficial relationship between irrigation, physical sward structure and arthropod diversity as found by Andrey et al. (2014) and Riedener et al. (2013) was not supported in the Queich meadows. Invertebrate sampling was only performed in the first year of the study when irrigation effects were also less pronounced for plant biodiversity measures. It is likely that distinct abiotic factors have interacted and thus covered the effect of irrigation on invertebrate diversity the same way as for the vegetation. The higher abundance of moisture-dependent species highlights the conservation value of the irrigated meadows as moist habitats and floodplains are highly under risk (Joyce and Wade 1998). Arthropod species are highly dependent on land use intensity and their diversity suffers from intense land use, which is mostly associated with fertilization (Simons et al. 2015, Chisté et al. 2016). Several arthropods and especially Orthopterans are not only important grassland herbivores having a regulative function for plant species communities but are also food sources for several higher trophic levels like birds, spiders and lizards (Ingrisch & Köhler 1998, Chisté 2016). Therefore, as irrigation did not harm Arthropod diversity in our study and was even beneficial in other studies (Riedener et al. 2013, Andrey et al. 2014), it could be an interesting management option for arthropod conservation. As intense grassland management is scarce in the region and thus the gradient of land use intensity is not very pronounced, a high biodiversity is supported at different trophic levels as they internally support each other (Scherber et al. 2010, Chisté et al. 2016 and citations therein). Traditional flood irrigation systems and the arrangement of the ditches aims to distribute the water homogeneously, but nevertheless the water distribution is still more or less patchy due to the microrelief of the meadows (Hassler 1995). Further, the installation of the ditches creates microhabitats of heterogeneous water and as follows nutrient availability. In the long run, the patchiness within the meadow as well as the heterogeneity of the irrigation systems are vital for the establishment and maintenance of biodiversity at different trophic levels but also biotic heterogeneity at the landscape scale.

Conclusions

Traditional flood irrigation offers a great potential for grassland multitrophic biodiversity conservation at different spatial scales. The maintenance of biotic heterogeneity in flood irrigated meadows highlights the conservation value of this traditional extensive management regime. The non-detrimental or even supporting influence of irrigation on biodiversity in contrast to fertilization is not only meaningful for the studied species groups, but will necessarily impact other trophic levels. Arthropods are a crucial food source for breeding and migratory birds and thus the maintenance of their diversity offers a great conservation value. Further, the significant changes in the plant community with a higher species diversity as well as structural heterogeneity suggests that irrigation in contrast to intensive fertilization does not reduce niche dimensionality as it sustains the multiple resource limitation and heterogeneity at the site (Tilman 1982, Harpole & Tilman 2007). Thus, irrigation proves to be less harmfull for biodiversity than intensive fertilization. The short-term water pulses as created by irrigation create complex patterns of heterogenous nutrient availability, which depends on the respective species growing at a site, but also the soil nutrient status, which in turn creates a direct feedback loop. The changes at the functional scale of the plant communities within irrigated meadows is thus not only a consequence of the biogeochemical processes triggered by irrigation, but also directly modifies ecosystem processes and interspecific competition fostering nutrient utilization efficiency. Although irrigation does not pose a direct fertilization effect anymore due to the lower nutrient load in the irrigation water, it still causes a secondary fertilization effect through the hot moment of nutrient availability during irrigation. Thus, irrigation during drier periods of the year could be a way to reduce fertilization intensity and improve nutrient utilization preventing high nutrient losses into non-target ecosystems. This could be a step towards the containment of overfertilization, but still, a concise adjustment of irrigation and fertilization, as well as the estimation of regional factors, is inevitable for the long-term positive contribution of irrigation to the local biodiversity and ecosystem processes. From the agronomic point of view, flood irrigation could support the maintenance of extensive management and thus builds a reasonable compromise between agricultural needs and biodiversity conservation.

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APPENDIX A

Chapter 2: Müller, I.B. et al. (2016). Plant functional shifts in Central European grassland under traditional flood irrigation. *Applied Vegetation Science*.

A. 1. Percent cover values (mean and SE) of sampled plant species in irrigated and non-irrigated meadows.

Tab. 1. Percent cover (mean and SE) of sampled plant species in the irrigated and non-irrigated meadows. Abbreviations of the species names were used in the NMDS ordination plot (Fig. 3). Nomenclature follows Wisskirchen & Haeupler 1998. Functional groups (FG) reflecting growth forms are obtained from CLO-PLA (Klimešová & Klimeš 2006, Třeboň, CZ) database. Reproduction types (RT) were taken from Biolflor traitbase (Klotz et al. 2002). r = rosette; sr = semi-rosette; sc = scaposa; g = graminoid; l = legume.s= sexual; v = vegetative. Differences in the mean cover of the species in irrigated versus non-irrigated meadows were tested for species occurring in ≥10% of the plots with quasi-Poisson GLMs. p<0.1; * = p<0.05; ** = p<0.01. ; *** = p<0.001. Irrigation affinity is based on the Spearman rank correlation coefficient of the respective species with irrigation.

Species	**Abbreviation**	**Cover (%)**		**Staticstics**		**Functional classification**	
		irrigated	**non-irrigate**	**t-value**	**Irrigation affinity**	**FG**	**RT**
Achillea millefolium	Achi.mille	1.02±0.45	4.2±0.78	-2.48*	-0.35	sr	sv
Achillea ptarmica	Achi.ptar	0.68±0.2	1.33±0.42	-1.33	-0.15	sc	sv
Agrimonia eupatoria	Agri.eupa	0.24±0.11	0.25±0.11	-0.03	0.00	sr	s
Agrostis capillaris	Agro.capi	0.22±0.17	0.06±0.06	0.78	0.08	g	sv
Ajuga reptans	Ajug.rept	0.97±0.36	0.89±0.31	0.09	0.02	sr	sv
Allium vineale	Alli.vine	0±0	0.001±0	n.t.	-0.12	r	v
Alopecurus pratensis	Alop.prat	8.39±1.06	6.44±1.11	0.75	0.12	g	sv
Anthoxanthum odoratum	Anth.odor	2.68±0.62	1.4±0.4	1.21	0.15	g	sv
Arrhenaterum elatius	Arrh.elat	11.61±1.36	14.76±1.22	-0.79	-0.16	g	ssv
Bellis perennis	Bell.peren	0.43±0.18	0.16±0.12	0.97	0.11	r	sv
Bromus hordeaceus	Brom.hord	0.38±0.11	0.15±0.12	0.82	0.14	g	s
Campanula patula	Camp.patu	0±0	0.003±0	n.t.	-0.21	sr	s
Cardamine pratensis	Card.prat	0.11±0.03	0.05±0.02	1.34	0.16	sr	vvs
Carex disticha	Care.dist	0.84±0.21	1.35±0.49	-0.94	-0.11	g	sv
Carex nigra	Care.nigr	0.09±0.06	0.35±0.21	-1.46	-0.13	g	sv
Carex praecox	Care.prae	0±0	0.12±0.08		-0.17	g	sv
Carex sylvatica	Care.sylv	0.09±0.06	0.12±0.08	-0.29	-0.03	g	sv
Centaurea jacea	Cent.jace	6.74±0.9	6.71±1.12	-0.02	0.00	sc	s
Centaurea nigra	Cent.nigr	0.06±0.04	0.13±0.08	-0.72	-0.08	sc	ssv
Cerastium fontanum	Cera.font	0.12±0.03	0.24±0.09	-1.04	-0.15	sc	sv
Cirsium arvense	Cirs.arve	1.16±0.29	1.24±0.34	-0.21	-0.02	sc	sv
Cirsium oleraceum	Cirs.oler	0±0	0.01±0.01	n.t.	-0.12	sr	sv
Colchicum autumnale	Colc.autu	0.7±0.23	1.19±0.4	-0.87	-0.11	sc	sv
Convolvulus arvensis	Conv.arve	0.01±0.01	0.14±0.08	-1.74.	-0.19	sr	vvs
Crepis capillaris	Crep.capi	0.03±0.01	0.04±0.02	-0.34	-0.04	sr	s

Species	**Abbreviation**	**Cover (%)**		**Staticstics**		**Functional classification**	
		irrigated	**non-irrigate**	**t-value**	**Irrigation affinity**	**FG**	**RT**
Cynosurus cristatus	Cyno.cris	0.96±0.25	0.04±0.02	1.75.	0.29	g	s
Dactylis glomerata	Dact.glom	6.57±0.8	14.26±1.3	-3.38**	-0.47	g	ssv
Daucus carota	Dauc.caro	0.13±0.13	1.96±0.78	-1.69.	-0.26	sr	s
Deschampsia cespitosa	Desc.cesp	2.18±0.49	5.4±1.04	-2.49*	-0.29	g	s
Elymus repens	Elym.repe	0.05±0	0±0	n.t.	0.10	g	vvs
Equisetum arvense	Equi.arve	0.01±0.04	0±0	n.t.	0.08	sc	sv
Festuca arundinacea	Fest.arun	2.97±0.01	0.01±0	0.00	0.35	g	s
Festuca pratensis	Fest.prat	3.07±0.67	3.73±0.01	-0.56	-0.08	g	s
Festuca rubra rubra	Fest.rubr	5.52±0.49	12.32±0.73	-2.58*	-0.38	g	sv
Filipendula ulmaria	Fili.ulma	0.14±1	0.17±1.39	-0.17	-0.02	sr	sv
Galium album	Gali.alb	9.75±0.07	16.57±0.08	-1.69	-0.28	sc	sv
Galium verum	Gali.veru	1.75±1.65	1.23±1.51	0.69	0.09	Sc	sv
Geranium pratense	Gera.prat	0.02±0.36	0.08±0.41	n.t.	-0.12	sr	sv
Glechoma hederacea	Glec.hede	0.22±0.01	0.87±0.06	-1.85*	-0.18	sc	sv
Helictotrichon pubescen	Heli.pube	0.84±0.1	1.06±0.39	-0.38	-0.04	g	sv
Heracleum sphondylium	Hera.spho	0.09±0.42	0.07±0.33	n.t.	0.02	sr	ssv
Holcus lanatus	Holc.lana	5.91±0.06	3.91±0.06	1.66	0.21	g	sv
Hypericum maculatum	Hype.macu	0±0.63	0.56±0.65	-0.70	-0.24	sc	sv
Iris sibirica	Iris.sibi	0.02±0	0±0.28	n.t.	0.12	sr	sv
Juncus effusus	Junc.efus	0.01±0.01	0.07±0	-1.32	-0.12	g	sv
Lathyrus pratensis	Lath.prat	0.88±0.01	0.9±0.06	-0.05	-0.01	sc	ssv
Leontodon autumnalis	Leon.autu	1.24±0.24	0.08±0.28	1.35	0.24	r	sv
Leontodon hispidus	Leon.hisp	0.18±0.39	0.94±0.06	-2.40*	-0.33	r	sv
Leucanthemum vulgare ircutianum	Leuc.vulg.ircu	0.28±0.07	0.77±0.24	-1.70.	-0.19	sr	sv
Leucanthemum vulgare praecox	Leuc.vulg.prae	0.02±0.1	0.07±0.27	n.t.	-0.10	sr	sv
Lolium perenne	Loli.pere	0.43±0.01	0.02±0.06	1.42	0.27	g	s
Luzula campestris	Luzu.camp	0±0.12	0.05±0.02	-1.96.	-0.24	g	sv
Lysimachia nummularia	Lysi.numu	0.52±0	0.47±0.02	0.17	0.02	sc	vvs
Lythrum salicaria	Lyth.sali	0.01±0.15	0±0.12	n.t.	0.09	sc	sv
Medicago lupulina	Medi.lupu	0.13±0.01	0±0	n.t.	0.12	l	sv
Mentha pulegium	Ment.pule	0.04±0.09	0±0	n.t.	0.08	sc	sv
Myosotis scorpioides scorpioides	Myos.scor.scor	0.17±0.04	0.13±0	0.17	0.02	sc	sv
Persicaria lapathifolia lapathifolia	Pers.lapa.lapa	0.51±0.1	0.07±0.12	1.35	0.17	sc	s
Persicaria maculosa	Pers.macu	0.36±0.21	0.27±0.06	0.33	0.04	sc	s
Phleum pratense	Phle.prat	1.47±0.14	0.42±0.11	0.96	0.15	g	ssv
Plantago lanceolata	Plan.lanc	7.62±0.57	4.51±0.22	1.80.	0.25	r	ssv
Plantago major major	Plan.majo	0±0.83	0±0.78	n.t.	0.08	r	ssv
Poa pratensis	Poa.prat	0.57±0	0.85±0	-0.92	-0.11	g	sv
Poa trivialis trivialis	Poa.triv.triv	1.63±0.13	2.69±0.22	-1.16	-0.16	g	sv
Ranunculus acris acris	Ranu.acri.acri	6.64±0.38	2.93±0.6	2.71*	0.37	sr	s
Ranunculus auricomus	Ranu.auri	0.03±0.65	0±0.62	0.004	0.16	sr	n.a.

Species	**Abbreviation**	**Cover (%)**		**Staticstics**		**Functional classification**	
		irrigated	**non-irrigate**	**t-value**	**Irrigation affinity**	**FG**	**RT**
Ranunculus ficaria bulbilifer	Ranu.fica.bulb	0.05±0.01	0.8±0	-2.07*	-0.23	sr	vvs
Ranunculus repens	Ranu.repe	9.74±0.02	3.05±0.38	2.60*	0.37	sr	sv
Rhinanthus minor	Rina.mino	0±1.33	0.02±0.56	n.t.	-0.17	sc	s
Rumex acetosa	Rume.acet	5.28±0	3.54±0.02	1.49	0.21	sr	sv
Rumex acetosella acetosella	Rume.acla.acla	0.1±0.58	0.08±0.52	n.t.	0.02	sr	sv
Rumex crispus	Rume.cris	0.39±0.06	0.23±0.06	1.11	0.11	sr	sv
Rumex obtusifolius	Rume.obtu	0.02±0.1	0.1±0.09	-1.57	-0.14	sr	ssv
Salvia pratensis	Salv.prat	0.01±0.01	0±0.06	n.t.	0.07	sr	ssv
Sanguisorba officinalis	Sang.offi	4.36±0.01	1.36±0	2.57*	0.37	sr	sv
Senecio jacobaea	Sene.jaco	0.01±0.59	0±0.32	n.t.	0.09	sr	ssv
Silaum silaus	Sila.sila	2.3±0.01	0.21±0	1.96.	0.28	sr	s
Silene flos-cuculi	Sile.fl-cu	0.55±0.58	1.64±0.07	-1.51	-0.20	sr	sv
Stellaria graminea	Stel.gram	0.06±0.22	0.35±0.57	-1.30	-0.13	sc	sv
Symphytum officinale bohemicum	Symp.offi.bohe	0.54±0.05	0.49±0.24	0.17	0.02	sr	ssv
Taraxacum officinale	Tara.offi	4.15±0.17	0.46±0.19	2.38*	0.37	r	s
Trifolium dubium	Trif.dubi	0.89±0.77	0.38±0.16	1.32	0.15	sc/l	s
Trifolium medium	Trif.medi	0.23±0.26	0.26±0.15	-0.12	-0.01	sr/l	sv
Trifolium pratense	Trif.prat	11.9±0.1	2.22±0.24	3.94***	0.51	sr/l	s
Trifolium repens	Trif.repe	1.73±1.29	0.08±0.62	1.66	0.31	l	sv
Trisetum flavescens	Tris.flav	0.24±0.43	0.97±0.07	-2.38*	-0.30	g	ssv
Veronica chamaedrys chamaedrys	Vero.cham.cham	0.48±0.12	0.54±0.21	-0.15	-0.02	sc	sv
Veronica serpyllifolia serpyllifolia	Vero.serp.serp	0.01±0.27	0.32±0.19	-1.84.	-0.25	sc	sv
Vicia hirsuta	Vici.hirs	1.09±0.01	1.1±0.14	0.08	0.00	sc/l	s
Vicia sativa nigra	Vici.sati.nigr	1.76±0.64	0.84±0.37	0.80	0.12	sc/l	s
Vicia sativa sativa	Vici.sati.sati	0.82±0.59	0.16±0.29	1.33	0.18	sc/l	s
Vicia sepium	Vici.sepi	0.89±0.29	0.37±0.05	1.69.	0.14	sc/l	ssv
Vicia tetrasperma	Vici.tetr	0.01±0.28	0.11±0.14	-1.86.	-0.19	sc/l	s

References

Wisskirchen, R. & Haeupler, H. 1998. *Standardliste der Farn- und Blütenpflanzen Deutschlands*. Ulmer, Stuttgart, DE.

A. 2. Moran’s I correlograms for the selected study sites

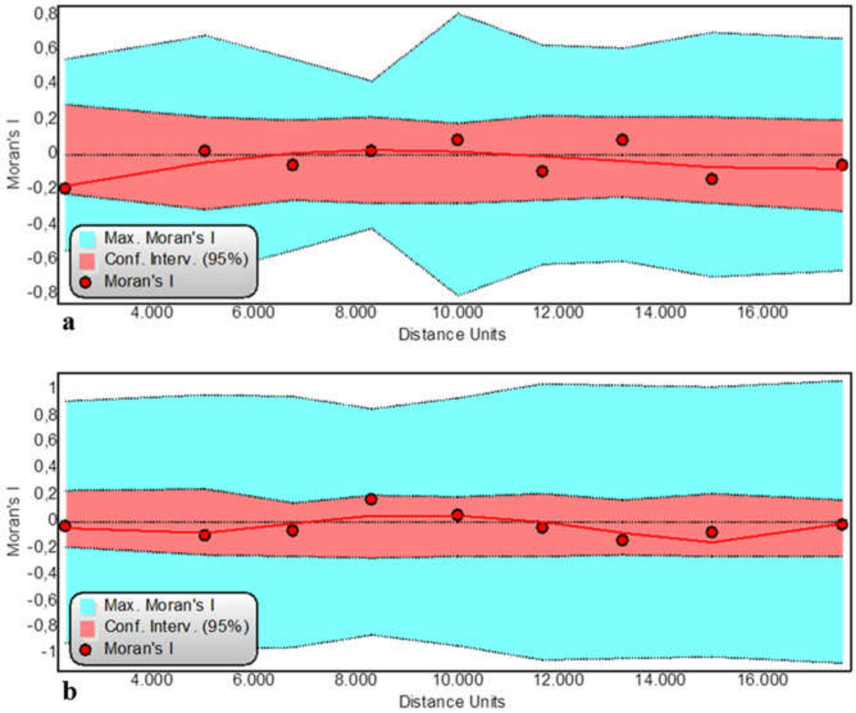

Fig. 1. Moran’s I correlograms of the explanatory variables in the n = 34 studied meadows. No significant autocorrelation was found for (a) irrigation ($p > 0.12$) and (b) fertilization ($p > 0.07$). Irrigation even tended to be negatively autocorrelated at the smallest scale, indicating that nearby meadows were more likely to be of different than of the same irrigation treatment.

APPENDIX B

Chapter 2: Müller, I.B. et al. (2016). Contrasting effects of irrigation and fertilization on plant diversity in hay meadows. *Basic and Applied Ecology*.

B. 1. Percent cover values (mean and SE) of sampled plant species in irrigated and non-irrigated meadows (2013 and 2013).

Tab. 1. Percent cover (mean and SE) of sampled plant species in irrigated and non-irrigated meadows in 2012 and 2013. The cover is the mean of two samplings per year (May and August).

	Mean cover (%) and ± SE			
	2012		**2013**	
Species	**irrigated**	**non-irrigated**	**irrigated**	**non-irrigated**
Achillea millefolium	1.02 ± 0.45	4.2 ± 0.78	1.94 ± 0.55	3.43 ± 1.34
Achillea ptarmica	0.68 ± 0.2	1.33 ± 0.42	1.05 ± 0.33	0.71 ± 0.28
Agrimonia eupatoria	0.24 ± 0.11	0.25 ± 0.11	0.08 ± 0.04	0.05 ± 0.03
Agrostis capillaris	0.22 ± 0.17	0.06 ± 0.06	0.4 ± 0.19	0.18 ± 0.13
Ajuga reptans	0.97 ± 0.36	0.89 ± 0.31	0.94 ± 0.29	1.22 ± 0.59
Allium vineale	0 ± 0	0.001 ± 0	0 ± 0	0 ± 0
Alopecurus pratensis	8.39 ± 1.06	6.44 ± 1.11	9.42 ± 2.05	17.96 ± 3.81
Anemone nemorosa	0 ± 0	0 ± 0	0.02 ± 0.02	0 ± 0
Anthoxanthum odoratum	2.68 ± 0.62	1.4 ± 0.4	3.97 ± 1.39	3.77 ± 0.99
Arrhenaterum elatius	11.61 ± 1.36	14.76 ± 1.22	13.91 ± 1.94	14.17 ± 2.27
Bellis perennis	0.43 ± 0.18	0.16 ± 0.12	0.29 ± 0.1	0.24 ± 0.09
Bromus hordeaceus	0.38 ± 0.11	0.15 ± 0.12	0.13 ± 0.04	0.29 ± 0.14
Campanula patula	0 ± 0	0.003 ± 0	0 ± 0	0.01 ± 0.01
Cardamine pratensis	0.11 ± 0.03	0.05 ± 0.02	0.37 ± 0.19	0.5 ± 0.38
Carex disticha	0.84 ± 0.21	1.35 ± 0.49	0.69 ± 0.23	1.22 ± 0.38
Carex nigra	0.09 ± 0.06	0.35 ± 0.21	0.2 ± 0.09	0.13 ± 0.13
Carex praecox	0 ± 0	0.12 ± 0.08	0.05 ± 0.04	0 ± 0
Carex sylvatica	0.09 ± 0.06	0.12 ± 0.08	0.02 ± 0.02	0.08 ± 0.04
Centaurea jacea	6.74 ± 0.9	6.71 ± 1.12	6 ± 1.08	6.49 ± 1.48
Centaurea nigra	0.06 ± 0.04	0.13 ± 0.08	0.08 ± 0.05	0.03 ± 0.03
Cerastium fontanum	0.12 ± 0.03	0.24 ± 0.09	0.33 ± 0.12	0.38 ± 0.15
Cirsium arvense	1.16 ± 0.29	1.24 ± 0.34	0.78 ± 0.37	1.64 ± 0.63
Cirsium oleraceum	0 ± 0	0.01 ± 0.01	0.02 ± 0.02	0 ± 0
Colchicum autumnale	0.7 ± 0.23	1.19 ± 0.4	1.48 ± 0.46	0.33 ± 0.11
Convolvulus arvensis	0.01 ± 0.01	0.14 ± 0.08	0.14 ± 0.1	0.05 ± 0.04
Crepis capillaris	0.03 ± 0.01	0.04 ± 0.02	0.04 ± 0.03	0.08 ± 0.08
Cynosurus cristatus	0.96 ± 0.25	0.04 ± 0.02	1.1 ± 0.4	1.15 ± 0.43
Dactylis glomerata	6.57 ± 0.8	14.26 ± 1.3	9.08 ± 1.27	10.88 ± 1.74

	Mean cover (%) and ± SE			
	2012		**2013**	
Species	**irrigated**	**non-irrigated**	**irrigated**	**non-irrigated**
Daucus carota	0.13 ± 0.13	1.96 ± 0.78	0.57 ± 0.39	0.21 ± 0.13
Deschampsia cespitosa	2.18 ± 0.49	5.4 ± 1.04	1.49 ± 0.5	2.21 ± 0.56
Elymus repens	0.05 ± 0	0 ± 0	0 ± 0	0.05 ± 0.05
Equisetum arvense	0.01 ± 0.04	0 ± 0	0 ± 0	0 ± 0
Festuca arundinacea	2.97 ± 0.01	0.01 ± 0	1.6 ± 0.74	2.26 ± 1.32
Festuca pratensis	3.07 ± 0.67	3.73 ± 0.01	4.24 ± 0.8	4.01 ± 1.1
Festuca rubra subsp. *rubra*	5.52 ± 0.49	12.32 ± 0.73	9.43 ± 2.17	8.13 ± 1.64
Filipendula ulmaria	0.14 ± 1	0.17 ± 1.39	0.21 ± 0.08	0.05 ± 0.05
Galium album	9.75 ± 0.07	16.57 ± 0.08	12.25 ± 2.14	9.76 ± 2.74
Galium verum	1.75 ± 1.65	1.23 ± 1.51	0.82 ± 0.27	1.3 ± 0.42
Geranium pratense	0.02 ± 0.36	0.08 ± 0.41	0.03 ± 0.03	0.08 ± 0.06
Glechoma hederacea	0.22 ± 0.01	0.87 ± 0.06	0.9 ± 0.25	0.73 ± 0.21
Helictotrichon pubescens	0.84 ± 0.1	1.06 ± 0.39	2.4 ± 1.08	0.59 ± 0.27
Heracleum sphondylium	0.09 ± 0.42	0.07 ± 0.33	0.13 ± 0.1	0 ± 0
Holcus lanatus	5.91 ± 0.06	3.91 ± 0.06	5.14 ± 0.67	7.17 ± 0.58
Hypericum maculatum	0 ± 0.63	0.56 ± 0.65	0.13 ± 0.1	0.05 ± 0.03
Iris sibirica	0.02 ± 0	0 ± 0.28	0.02 ± 0.02	0.03 ± 0.03
Juncus effusus	0.01 ± 0.01	0.07 ± 0	0.02 ± 0.02	0 ± 0
Lathyrus pratensis	0.88 ± 0.01	0.9 ± 0.06	1.6 ± 0.34	0.95 ± 0.28
Leontodon autumnalis	1.24 ± 0.24	0.08 ± 0.28	1.48 ± 0.87	0.79 ± 0.72
Leontodon hispidus	0.18 ± 0.39	0.94 ± 0.06	0.71 ± 0.24	0.15 ± 0.06
Leucanthemum vulgare subsp. *ircutianum*	0.28 ± 0.07	0.77 ± 0.24	0.44 ± 0.17	0.49 ± 0.2
Leucanthemum vulgare subsp. *praecox*	0.02 ± 0.1	0.07 ± 0.27	0.02 ± 0.02	0.08 ± 0.04
Lolium perenne	0.43 ± 0.01	0.02 ± 0.06	0.2 ± 0.11	0.49 ± 0.22
Luzula campestris	0 ± 0.12	0.05 ± 0.02	0.03 ± 0.02	0 ± 0
Lysimachia nummularia	0.52 ± 0	0.47 ± 0.02	0.48 ± 0.16	0.71 ± 0.3
Lythrum salicaria	0.01 ± 0.15	0 ± 0.12	0.05 ± 0.03	0.03 ± 0.03
Medicago lupulina	0.13 ± 0.01	0 ± 0	0.09 ± 0.05	0.18 ± 0.05
Mentha pulegium	0.04 ± 0.09	0 ± 0	0 ± 0	0.1 ± 0.1
Myosotis scorpioides subsp. *scorpioides*	0.17 ± 0.04	0.13 ± 0	0.29 ± 0.22	0 ± 0
Persicaria lapathifolia subsp. *lapathifolia*	0.51 ± 0.1	0.07 ± 0.12	0.1 ± 0.03	0.46 ± 0.31
Persicaria maculosa	0.36 ± 0.21	0.27 ± 0.06	0.43 ± 0.19	0.4 ± 0.17
Phleum pratense	1.47 ± 0.14	0.42 ± 0.11	0.83 ± 0.37	2.08 ± 1.37
Plantago lanceolata	7.62 ± 0.57	4.51 ± 0.22	6.17 ± 1	4.79 ± 1.23
Plantago major subsp. *major*	0 ± 0.83	0 ± 0.78	0.02 ± 0.02	0 ± 0
Poa pratensis	0.57 ± 0	0.85 ± 0	1.27 ± 0.34	1.46 ± 0.41
Poa trivialis trivialis	1.63 ± 0.13	2.69 ± 0.22	2.2 ± 0.48	3.28 ± 0.64
Ranunculus acris subsp. *acris*	6.64 ± 0.38	2.93 ± 0.6	5.07 ± 1.04	4.75 ± 0.74
Ranunculus auricomus	0.03 ± 0.65	0 ± 0.62	0.04 ± 0.02	0.03 ± 0.03
Ranunculus ficaria subsp. *bulbilifer*	0.05 ± 0.01	0.8 ± 0	0.38 ± 0.15	1.26 ± 0.83
Ranunculus repens	9.74 ± 0.02	3.05 ± 0.38	7.84 ± 1.65	6.64 ± 2.08
Rhinanthus minor	0 ± 1.33	0.02 ± 0.56	0.08 ± 0.08	0 ± 0
Rumex acetosa	5.28 ± 0	3.54 ± 0.02	4.35 ± 0.72	5.71 ± 0.73
Rumex acetosella subsp. *acetosella*	0.1 ± 0.58	0.08 ± 0.52	0.08 ± 0.06	0.31 ± 0.25

	Mean cover (%) and ± SE			
	2012		**2013**	
Species	**irrigated**	**non-irrigated**	**irrigated**	**non-irrigated**
Rumex crispus	0.39 ± 0.06	0.23 ± 0.06	0.5 ± 0.19	0.34 ± 0.15
Rumex obtusifolius	0.02 ± 0.1	0.1 ± 0.09	0.1 ± 0.05	0.03 ± 0.03
Salvia pratensis	0.01 ± 0.01	0 ± 0.06	0 ± 0	0 ± 0
Sanguisorba officinalis	4.36 ± 0.01	1.36 ± 0	3 ± 0.61	1.9 ± 0.64
Senecio jacobaea	0.01 ± 0.59	0 ± 0.32	0 ± 0	0.08 ± 0.04
Silaum silaus	2.3 ± 0.01	0.21 ± 0	1.01 ± 0.43	1.67 ± 0.62
Silene flos-cuculi	0.55 ± 0.58	1.64 ± 0.07	1.54 ± 0.31	0.9 ± 0.2
Stellaria graminea	0.06 ± 0.22	0.35 ± 0.57	0.06 ± 0.04	0.09 ± 0.06
Symphytum officinale subsp. *bohemicum*	0.54 ± 0.05	0.49 ± 0.24	0.82 ± 0.33	0.38 ± 0.16
Taraxacum officinale s.l.	4.15 ± 0.17	0.46 ± 0.19	2.66 ± 0.87	1.9 ± 1.12
Trifolium dubium	0.89 ± 0.77	0.38 ± 0.16	0.64 ± 0.22	0.57 ± 0.32
Trifolium medium	0.23 ± 0.26	0.26 ± 0.15	0.07 ± 0.03	0.03 ± 0.03
Trifolium pratense	11.9 ± 0.1	2.22 ± 0.24	7.6 ± 1.75	5.87 ± 1.65
Trifolium repens	1.73 ± 1.29	0.08 ± 0.62	1.42 ± 0.7	0.79 ± 0.38
Trisetum flavescens	0.24 ± 0.43	0.97 ± 0.07	0.94 ± 0.24	1.02 ± 0.36
Veronica chamaedrys subsp. *chamaedrys*	0.48 ± 0.12	0.54 ± 0.21	0.37 ± 0.15	0.62 ± 0.36
Veronica serpyllifolia subsp. *serpyllifolia*	0.01 ± 0.27	0.32 ± 0.19	0.19 ± 0.1	0.11 ± 0.06
Vicia hirsuta	1.09 ± 0.01	1.1 ± 0.14	0.7 ± 0.29	1.28 ± 0.84
Vicia sativa subsp. *nigra*	1.76 ± 0.64	0.84 ± 0.37	1.13 ± 0.32	1.94 ± 1.09
Vicia sativa subsp. *sativa*	0.82 ± 0.59	0.16 ± 0.29	0.77 ± 0.3	1.18 ± 0.45
Vicia sepium	0.89 ± 0.29	0.37 ± 0.05	0.75 ± 0.29	0.18 ± 0.13
Vicia tetrasperma	0.01 ± 0.28	0.11 ± 0.14	0.13 ± 0.05	0.03 ± 0.03

B. 2. Effects of irrigation on plant α-diversity.

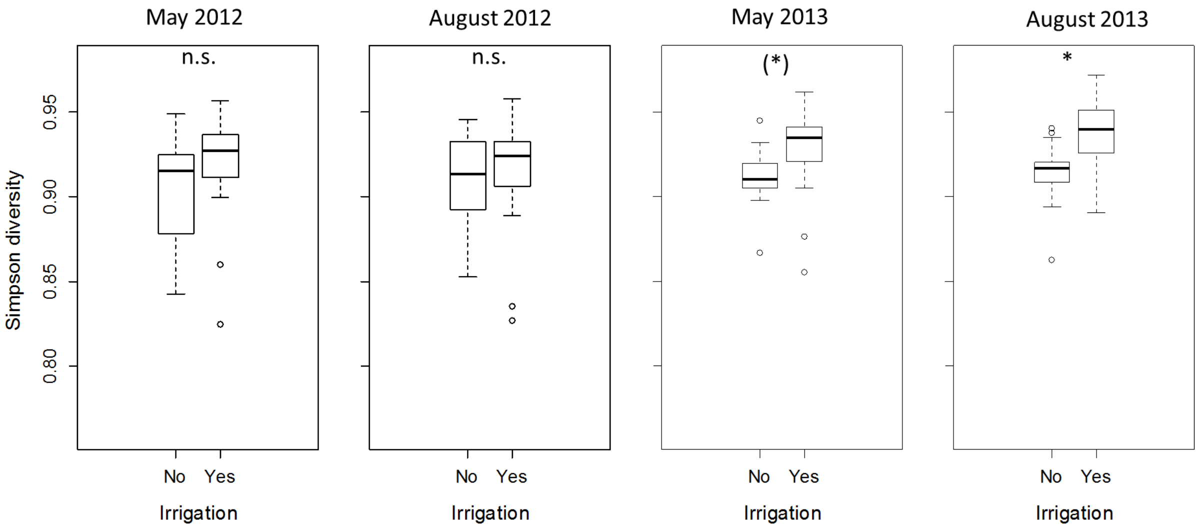

Fig. 1. Effects of meadow irrigation on Simpson diversity of plants in May 2012 and 2013 and September 2012 and 2013. Significance was tested with linear models and permutational ANOVA. n.s. not significant, (*) P < 0.1, * P < 0.05, ** P < 0.01.

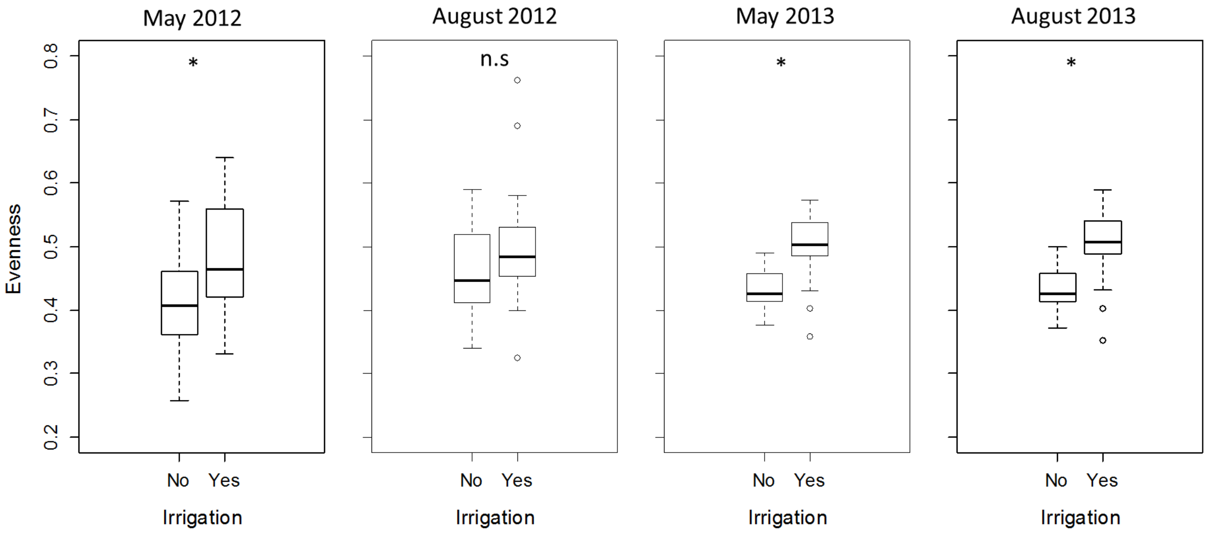

Fig. 2. Effects of meadow irrigation on Evenness of plants in May 2012 and 2013 and September 2012 and 2013. Significance was tested with linear models and permutational ANOVA. n.s. not significant, (*) P < 0.1, * P < 0.05, ** P < 0.01.

APPENDIX C

Chapter 4: Schirmel, J. et al. (2014). Effects of Traditional Flood Irrigation on Invertebrates in Lowland Meadows. *PLoS ONE*.

C. 1. Moisture indicator values of Orthoptera.

Tab. 1. Moisture indicator values of Orthoptera based on information in Maas et al. (2002). Information was coded numerically as follows: Strongly xerophilic = 1, xerophilic = 2, mesophilic = 3, hygrophilic = 4, strongly hygrophilic = 5.

Species	Maas et al. (2002)	Moisture indicator value
Aiolopus thalassinus	Hygrophilic	4
Chorthippus biguttulus	Xerophilic	2
Chorthippus dorsatus	Mesophilic-hygrophilic	3.5
Chorthippus parallelus	Mesophilic-hygrophilic	3.5
Mecostethus parapleurus	Hygrophilic	4
Metrioptera roeselii	Mesophilic-hygrophilic	3.5
Stetophyma grossum	Strongly hygrophilic	5

C. 2. Abundances (mean and SE) of Orthoptera, carabid, and spider species in irrigated and non-irrigated meadows.

Tab. 1. Abundances (mean and SE) of Orthoptera, carabid, and spider species in irrigated and non-irrigated meadows in the Queichtal, Rhineland-Palatine (Germany). Differences were tested with Poisson or, in case of overdispersion, quasi-Poisson GLM's for count data (only species with ≥ 10 individuals). n.t. = not tested. Significant results ($P < 0.05$) are shown in bold.

Species	**Abundance**		**Statistics**	
	Irrigated	**Non-irrigated**	**t/z**	**P**
Orthoptera				
Aiolopus thalassinus	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Chorthippus biguttulus	2.6 ± 1.0	4.8 ± 1.9	t = -1.051	0.302
Chorthippus dorsatus	5.9 ± 2.6	7.3 ± 1.8	t = -0.428	0.672
Chorthippus parallelus	1.3 ± 0.4	1.8 ± 0.5	t = -0.653	0.519
Mecostethus parapleurus	2.3 ± 0.8	0.4 ± 0.1	t = 2.492	**0.019**
Metrioptera roeselii	0.6 ± 0.3	0.1 ± 0.1	z = 2.084	**0.037**
Stetophyma grossum	4.2 ± 1.0	1.8 ± 0.5	t = 2.091	**0.045**
Carabids				
Abax parallelepipedus	0.1 ± 0.1	0 ± 0	n.t.	
Agonum muelleri	0.1 ± 0.1	0 ± 0	n.t.	
Agonum viduum	0.1 ± 0.1	0 ± 0	n.t.	
Amara aenea	1.4 ± 0.7	3.6 ± 1.5	t = -1.313	0.200
Amara communis	1.1 ± 0.4	0.9 ± 0.4	t = 0.486	0.631
Amara familiaris	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Amara kultii	0.8 ± 0.3	0.7 ± 0.4	t = 0.136	0.893
Amara lunicollis	4.0 ± 0.9	3.1 ± 0.7	t = 0.806	0.428
Amara plebeja	0.1 ± 0.1	0 ± 0	n.t.	
Amara similata	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Amara strenuua	0.4 ± 0.3	0 ± 0	n.t.	
Amara tibialis	0 ± 0	0.1 ± 0.1	n.t.	
Anisodactylus binotatus	3.1 ± 0.9	2.3 ± 1.5	t = 0.475	0.639
Bembidion guttula	2.4 ± 0.9	0.2 ± 0.2	t = 2.369	**0.026**
Bembidion lampros	0.4 ± 0.3	0 ± 0	n.t.	
Bembidion properans	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Bembidion quadrimaculatum	0 ± 0	0.1 ± 0.1	n.t.	
Brachinus explodens	0.1 ± 0.1	0 ± 0	n.t.	
Carabus cancellatus	0.5 ± 0.3	0.4 ± 0.4	t = 0.160	0.874
Carabus granulatus	0.9 ± 0.3	0.1 ± 0.1	t = 2.255	**0.033**
Carabus nemoralis	0 ± 0	0.1 ± 0.1	n.t.	

Carabus violaceus	0.1 ± 0.1	0 ± 0	n.t.	
Chlaenius nigricornis	0.3 ± 0.2	0 ± 0	n.t.	
Clivina collaris	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Clivina fossor	0.6 ± 0.2	0.3 ± 0.2	t = 0.870	0.392
Diachromus germanus	0.1 ± 0.1	0 ± 0	n.t.	
Dyschirius globosus	0.4 ± 0.3	0.1 ± 0.1	n.t.	
Harpalus affinis	0.4 ± 0.1	0.4 ± 0.2	z = 0.000	1.000
Harpalus anxius	0.3 ± 0.2	0 ± 0	n.t.	
Harpalus distinguendes	0.3 ± 0.1	0.1 ± 0.1	n.t.	
Harpalus latus	0.2 ± 0.2	0.4 ± 0.2	n.t.	
Harpalus luteicornis	0.2 ± 0.2	0.9 ± 0.3	t = -1.935	0.064
Harpalus rubripes	0 ± 0	0.1 ± 0.1	n.t.	
Loricera pililcornis	0.1 ± 0.1	0 ± 0	n.t.	
Microlestes minutulus	0.2 ± 0.2	0 ± 0	n.t.	
Oodes helopioides	0.4 ± 0.3	0 ± 0	n.t.	
Ophonus ardosiacus	0 ± 0	0.1 ± 0.1	n.t.	
Poecilus cupreus	11.1 ± 4.4	2.6 ± 1.2	t = 1.985	0.058
Poecilus versicolor	25.9 ± 6.8	21.7 ± 5.4	t = 0.479	0.636
Pseudophonus rufipes	0 ± 0	0.2 ± 0.1	n.t.	
Pterostichus anthracinus	0.1 ± 0.1	0 ± 0	n.t.	
Pterostichus diligens	0.2 ± 0.1	0.4 ± 0.3	n.t.	
Pterostichus melanarius	1.9 ± 0.7	1.6 ± 0.6	t = 0.318	0.753
Pterostichus strenuus	0.1 ± 0.1	0 ± 0	n.t.	
Pterostichus vernalis	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Stomis pumicatus	0 ± 0	0.1 ± 0.1	n.t.	
Syntomus truncatellus	0.4 ± 0.2	0.7 ± 0.3	t = -0.870	0.392
Spiders				
Agyneta affinis	1.1 ± 0.4	1.9 ± 0.7	t = -0.997	0.328
Agyneta rurestris	1.0 ± 0.3	1.4 ± 0.6	t = -0.554	0.584
Alopecosa cuneata	20.9 ± 6.7	23.4 ± 5.0	t = -0.307	0.761
Alopecosa pulverulenta	0.1 ± 0.1	0 ± 0	n.t.	
Araeoncus humilis	0.1 ± 0.1	0 ± 0	n.t.	
Arctosa leopardus	8.5 ± 3.6	0.4 ± 0.3	t = 2.094	**0.046**
Arctosa lutetiana	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Arctosa perita	0.1 ± 0.1	0 ± 0	n.t.	
Aulonia albimana	0 ± 0	0.4 ± 0.2	n.t.	
Bathyphantes gracilis	0 ± 0	0.1 ± 0.1	n.t.	
Ceratinella brevipes	0.6 ± 0.4	0.7 ± 0.3	t = -0.268	0.791
Cnephalocotes obscurus	0.1 ± 0.1	0 ± 0	n.t.	
Dendryphantes rudis	0 ± 0	0.1 ± 0.1	n.t.	

Dicymbium nigrum	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Diplostyla concolor	0.3 ± 0.2	0.1 ± 0.1	n.t.	
Drassyllus lutetianus	0.2 ± 0.1	0.1 ± 0.1	n.t.	
Drassyllus praeficus	0.1 ± 0.1	0.2 ± 0.2	n.t.	
Drassyllus pusillus	0.4 ± 0.2	1.1 ± 0.6	t = -1.112	0.276
Erigone atra	2.4 ± 0.8	1.0 ± 0.5	t = 1.397	0.174
Erigone dentipalpis	2.3 ± 0.6	4.1 ± 2.6	t = -0.772	0.447
Hahnia nava	1.2 ± 0.5	0.8 ± 0.5	t = 0.570	0.574
Haplodrassus signifer	0 ± 0	0.1 ± 0.1	n.t.	
Mermessus trilobatus	0.2 ± 0.1	1.7 ± 1.0	t = -1.646	0.112
Micaria pulicaria	0 ± 0	0.1 ± 0.1	n.t.	
Oedothorax fuscus	31.5 ± 9.5	3.0 ± 1.3	t = 2.968	**0.006**
Oedothorax retusus	6.9 ± 3.0	1.1 ± 0.1	t = 1.913	0.067
Ozyptila simplex	2.9 ± 0.9	2.4 ± 1.1	t = 0.356	0.725
Pachygnatha clercki	1.8 ± 0.8	0.1 ± 0.1	t = 1.77	0.088
Pachygnatha degeeri	15.9 ± 3.1	11.1 ± 2.7	t = 1.168	0.253
Pardosa cf agrestis	0.5 ± 0.4	0 ± 0	n.t.	
Pardosa amentata	0.3 ± 0.2	0.4 ± 0.1	n.t.	
Pardosa hortensis	0 ± 0	0.1 ± 0.1	n.t.	
Pardosa lugubris	0.1 ± 0.1	0 ± 0	n.t.	
Pardosa palustris	109.0 ± 20.1	70.7 ± 17.9	t = 1.375	0.181
Pardosa prativaga	8.1 ± 2.5	3.4 ± 1.7	t = 1.505	0.144
Pardosa pullata	30.3 ± 6.6	24.2 ± 5.8	t = 0.694	0.494
Pelecopsis parallela	2.8 ± 1.0	3.1 ± 1.7	t = -0.145	0.886
Phrurolithus festivus	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Phrurolithus minimus	0 ± 0	0.1 ± 0.1	n.t.	
Pirata latitans	0.1 ± 0.1	0 ± 0	n.t.	
Pirata piraticus	0.3 ± 0.2	0.1 ± 0.1	n.t.	
Pirata uliginosus	0.4 ± 0.2	0.5 ± 0.4	t = -0.150	0.882
Tenuiphantes tenius	0.1 ± 0.1	0 ± 0	n.t.	
Thanatus striatus	0 ± 0	0.1 ± 0.1	n.t.	
Tiso vagans	0.1 ± 0.1	0.1 ± 0.1	n.t.	
Trachyzelotes pedestris	0.1 ± 0.1	0.2 ± 0.2	n.t.	
Trochosa ruricola	21.1 ± 3.7	12.8 ± 2.6	t = 1.869	0.073
Trochosa spinipalpis	0.2 ± 0.2	0 ± 0	n.t.	
Trochosa terricola	0.4 ± 0.2	0.8 ± 0.4	t = -0.900	0.376
Walckenaeria antica	0 ± 0	0.1 ± 0.1	n.t.	
Xerolycosa miniata	1.4 ± 0.6	2.3 ± 1.2	t = -0.708	0.485
Xysticus acerbus	1.6 ± 0.4	0.7 ± 0.3	t = 1.874	0.072
Xysticus audax	0.3 ± 0.1	0.3 ± 0.2	n.t.	
Xysticus cristatus	0.5 ± 0.2	0.3 ± 0.2	t = 0.702	0.489

Xysticus kochi	0.4 ± 0.2	0.3 ± 0.2	t = 0.547	0.589
Zelotes latreillei	0.1 ± 0.1	0 ± 0	n.t.	

C. 3. Site characteristics.

Tab. 1. Site characteristics and management factors of the study sites.

Plot Id	x	y	Irrigation	Fertilization	Distance to permanent water [m]	Distance to forest [m]	Humidity	Nitrogen
1-01-a	440119,65	5450296,47	yes	yes	203	130	5,83	5,40
1-02-a	442300,00	5450782,00	yes	yes	88	61	5,69	5,61
1-03-a	442974,37	5450377,51	yes	yes	684	84	5,83	5,05
1-04-a	442883,60	5450863,09	yes	yes	215	137	5,45	5,29
1-08-a	444934,00	5450805,00	yes	yes	80	71	5,98	5,63
1-09-a	445282,91	5451473,93	yes	yes	160	55	5,66	5,35
2-02-a	446395,00	5450898,00	yes	yes	716	165	5,70	5,27
3-02-a	440521,38	5450779,82	yes	yes	590	68	5,86	5,80
3-04-a	446822,59	5450857,02	yes	yes	1100	140	5,64	5,33
1-04-b	443024,75	5450613,10	yes	no	450	95	5,59	5,89
1-05-a	443803,00	5450380,42	yes	no	737	56	5,86	5,09
1-05-b	444742,00	5450338,00	yes	no	407	40	5,52	5,64
1-06-a	444858,48	5450193,87	yes	no	494	55	5,34	5,82
1-07-b	444628,04	5451087,24	yes	no	97	93	6,22	5,84
3-03-a	444173,62	5451238,30	yes	no	187	182	6,17	4,91
3-04-c	446909,00	5450993,00	yes	no	1230	265	5,94	5,87
5-05-b	442297,67	5451085,00	no	yes	157	160	5,84	5,80
5-05-c	443130,82	5451403,30	no	yes	190	38	5,61	5,14
5-06-a	443214,78	5450628,43	no	yes	488	55	5,48	5,23
5-07-a	447181,62	5452342,49	no	yes	58	56	5,42	5,98
5-07-b	447750,00	5452204,00	no	yes	188	55	5,32	5,21
5-11-a	445472,00	5449688,00	no	yes	583	233	5,76	4,86
5-11-b	445184,00	5450037,00	no	yes	675	75	5,49	5,07
5-13-b	446880,00	5451195,00	no	yes	1285	136	5,69	5,61
5-03-a	439372,42	5450103,82	no	no	63	42	5,85	5,17
5-05-a	443851,34	5451497,59	no	no	167	231	5,57	5,35
5-08-a	443979,73	5452477,74	no	no	85	47	5,97	5,96
5-08-b	444286,98	5452617,65	no	no	198	75	5,62	5,00
5-09-a	444466,20	5451955,01	no	no	545	144	5,69	5,09
5-10-a	444812,00	5451322,00	no	no	100	56	5,94	5,52
5-12-a	446013,00	5450841,00	no	no	350	39	5,76	5,42
5-13-a	447913,82	5451089,43	no	no	1195	53	5,26	5,59

C. 4. Additional data.

Tab. 1. Count data of Orthopteran species in irrigated and non-irrigated meadows.

plot	*Aiolopus thalassinus*	*Chorthippus biguttulus*	*Chorthippus dorsatus*	*Chorthippus parallelus*	*Mecostethus parapleurus*	*Metrioptera roeselii*	*Stetophyma grossum*
1-01-a	0	0	1	0	7	0	3
1-02-a	0	0	0	0	0	0	1
1-03-a	0	10	25	2	0	4	0
1-04-a	0	5	7	3	4	3	3
1-08-a	0	0	2	2	12	0	6
1-09-a	0	0	0	0	0	0	6
2-02-a	0	0	0	1	1	0	8
3-02-a	0	4	4	5	3	1	4
3-04-a	0	0	3	0	3	0	13
1-04-b	0	2	3	0	0	0	0
1-05-a	0	0	4	3	2	1	8
1-05-b	0	4	37	4	0	0	10
1-06-a	1	14	5	0	1	0	1
1-07-b	0	0	0	0	1	0	0
3-03-a	0	0	0	0	2	0	0
3-04-c	0	2	3	1	0	0	4
5-05-b	0	2	0	1	0	0	3
5-05-c	0	2	3	1	0	0	2
5-06-a	0	3	13	7	1	0	0
5-07-a	0	0	8	0	1	0	0
5-07-b	0	2	10	0	0	0	0
5-11-a	2	30	12	1	0	0	0
5-11-b	0	8	25	3	0	0	0
5-13-b	0	15	7	0	1	0	5
5-03-a	0	5	6	1	0	0	3
5-05-a	0	2	2	0	0	0	2
5-08-a	0	0	3	3	0	0	4
5-08-b	0	0	1	0	0	0	0
5-09-a	0	0	1	2	1	0	0
5-10-a	0	0	2	5	1	0	3
5-12-a	0	6	3	4	0	0	7
5-13-a	0	2	20	0	1	1	0

Tab. 2. Count data of Carabid species in irrigated and non-irrigated meadows.

plot	Abax.parallelepipedus	Agonum.muelleri	Agonum.viduum	Amara.aenea	Amara.communis	Amara.familiaris	Amara.kultii	Amara.lunicollis	Amara.plebeja	Amara.similata	Amara.strenuua	Amara.tibialis	Anisodactylus.binotatus	Bembidion.guttula	Bembidion.lampros	Bembidion.properans	Bembidion.quadrimaculatum	Brachinus.explodens	Carabus.cancellatus	Carabus.granulatus	Carabus.nemoralis	Carabus.violaceus	Chlaenius.nigricornis	Clivina.collaris	Clivina.fossor	Diachromus.germanus	Dyschirius.globosus	Harpalus.affinis	Harpalus.anxius	Harpalus.distinguendes	Harpalus.latus	Harpalus.luteicornis	Harpalus.rubripes	Loricera.pililcornis	Microlestes.minutulus	Oodes.helopioides	Ophonus.ardosiacus	Poecilus.cupreus	Poecilus.versicolor	Pseudophonus.rufipes	Pterostichus.anthracinus	Pterostichus.diligens	Pterostichus.melanarius	Pterostichus.strenuus	Pterostichus.vernalis	Stomis.pumicatus	Syntomus.truncatellus
1-01a	0	0	0	1	1	0	0	1	0	0	0	0	10	8	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	34	12	0	0	0	9	0	0	0	0
1-03-	1	0	0	2	0	0	3	2	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	3	0	0	0	0	0	0	1	13	0	0	0	4	0	0	0	0
1-08a	0	1	1	0	0	0	0	1	0	0	0	0	2	4	3	0	0	0	1	2	0	1	2	0	1	0	3	1	0	1	0	0	0	1	0	0	0	13	28	0	0	0	1	0	0	0	0
1-09a	0	0	0	0	1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1	0	24	93	0	1	0	2	0	0	0	1
2-02a	0	0	0	0	4	1	0	5	1	0	2	0	1	7	2	0	0	0	3	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0	5	64	0	0	1	0	0	0	0	0
3-02a	0	0	0	0	0	0	2	12	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	13	20	0	0	0	5	0	0	0	0
3-04a	0	0	0	2	1	0	1	3	0	0	0	0	7	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	43	0	0	0	0	0	0	0	0
1-04b	0	0	0	10	1	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	1
1-05a	0	0	0	0	0	0	2	5	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	0	0	0	1	6	0	0	0	1	0	0	0	0

plot	***Abax.parallelepipedus***	***Agonum.muelleri***	***Agonum.viduum***	***Amara.aenea***	***Amara.communis***	***Amara.familiaris***	***Amara.kultii***	***Amara.lunicollis***	***Amara.plebeja***	***Amara.similata***	***Amara.strenuua***	***Amara.tibialis***	***Anisodactylus.binotatus***	***Bembidion.guttula***	***Bembidion.lampros***	***Bembidion.properans***	***Bembidion.quadrimaculatum***	***Brachinus.explodens***	***Carabus.cancellatus***	***Carabus.granulatus***	***Carabus.nemoralis***	***Carabus.violaceus***	***Chlaenius.nigricornis***	***Clivina.collaris***	***Clivina.fossor***	***Diachromus.germanus***	***Dyschirius.globosus***	***Harpalus.affinis***	***Harpalus.anxius***	***Harpalus.distinguendes***	***Harpalus.latus***	***Harpalus.luteicornis***	***Harpalus.rubripes***	***Loricera.pililcornis***	***Microlestes.minutulus***	***Oodes.helopioides***	***Ophonus.ardosiacus***	***Poecilus.cupreus***	***Poecilus.versicolor***	***Pseudophonus.rufipes***	***Pterostichus.anthracinus***	***Pterostichus.diligens***	***Pterostichus.melanarius***	***Pterostichus.strenuus***	***Pterostichus.vernalis***	***Stomis.pumicatus***	***Syntomus.truncatellus***
1-05b	0	0	0	0	3	0	0	7	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	8	0	0	0	0	1	1	0	0
1-06a	0	0	0	4	3	0	1	10	0	0	1	0	6	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	7	23	0	0	0	0	0	0	0	3
1-07b	0	1	0	0	0	0	0	1	0	0	3	0	2	6	0	1	0	0	0	2	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	1	0	55	28	0	0	1	3	0	0	0	0
3-03a	0	0	0	0	2	0	0	3	0	0	0	0	1	7	0	0	0	0	0	3	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1	0	1	12	0	0	1	0	0	0	0	0
3-04c	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	2	0	0	0	0
5-05b	0	0	0	2	0	0	0	7	0	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	23	0	0	0	1	0	0	0	0
5-06a	0	0	0	11	0	0	4	5	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	28	0	0	0	0	0	0	0	3
5-07a	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	2	15	0	0	0	6	0	0	0	4
5-07b	0	0	0	4	4	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
5-11a	0	0	0	2	0	0	5	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	1

plot	Abax.parallelepipedus	Agonum.muelleri	Agonum.viduum	Amara.aenea	Amara.communis	Amara.familiaris	Amara.kultii	Amara.lunicollis	Amara.plebeja	Amara.similata	Amara.strenuua	Amara.tibialis	Anisodactylus.binotatus	Bembidion.guttula	Bembidion.lampros	Bembidion.properans	Bembidion.quadrimaculatum	Brachinus.explodens	Carabus.cancellatus	Carabus.granulatus	Carabus.nemoralis	Carabus.violaceus	Chlaenius.nigricornis	Clivina.collaris	Clivina.fossor	Diachromus.germanus	Dyschirius.globosus	Harpalus.affinis	Harpalus.anxius	Harpalus.distinguendes	Harpalus.latus	Harpalus.luteicornis	Harpalus.rubripes	Loricera.pililcornis	Microlestes.minutulus	Oodes.helopioides	Ophonus.ardosiacus	Poecilus.cupreus	Poecilus.versicolor	Pseudophonus.rufipes	Pterostichus.anthracinus	Pterostichus.diligens	Pterostichus.melanarius	Pterostichus.strenuus	Pterostichus.vernalis	Stomis.pumicatus	Syntomus.truncatellus
5-11b	0	0	0	21	0	0	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0
5-13b	0	0	0	4	1	1	0	7	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0	1	2	0	0	0	0	0	3	7	0	0	1	1	0	0	0	0
5-03a	0	0	0	1	0	0	0	2	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1	0	0	0	0	0	2	4	0	0	0	1	0	0	1	0
5-08a	0	0	0	0	2	0	0	1	0	0	0	0	4	2	0	0	0	0	0	1	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	0	7	38	0	0	3	4	0	1	0	0
5-08b	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	27	0	0	0	0	0	0	0	0
5-09a	0	0	0	2	5	0	0	4	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	0	0	16	35	1	0	0	4	0	0	0	0
5-10a	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0	0	0	4	64	1	0	0	5	0	0	0	0
5-12a	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	53	1	0	2	1	0	1	0	0
5-13a	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Tab. 3. Count data of Araneae species in irrigated and non-irrigated meadows.

plot	**1-01a**	**1-03a**	**1-08a**	**1-09a**	**2-02a**	**3-02a**	**3-04a**	**1-04b**	**1-05a**	**1-05b**
Alopecosa.cuneata	2	54	4	90	3	10	27	27	3	22
Alopecosa.pulverulenta	0	0	0	0	0	0	0	0	0	1
Araeoncus.humilis	0	0	1	0	0	0	0	0	0	0
Arctosa.leopardus	22	0	7	3	2	1	22	0	47	0
Arctosa.lutetiana	0	0	0	1	0	0	0	0	1	0
Arctosa.perita	0	0	0	0	0	0	0	0	0	0
Aulonia.albimana	0	0	0	0	0	0	0	0	0	0
Bathyphantes.gracilis	0	0	0	0	0	0	0	0	0	0
Ceratinella.brevipes	0	0	2	0	0	0	0	0	0	0
Cnephalocotes.obscuru	0	0	0	1	0	0	0	0	0	0
Dendryphantes.rudis	0	0	0	0	0	0	0	0	0	0
Dicymbium.nigrum	0	0	0	0	0	0	0	0	0	0
Diplostyla.concolor	0	0	0	0	0	2	0	2	0	0
Drassyllus.lutetianus	0	0	0	0	0	0	0	1	0	0
Drassyllus.praeficus	0	0	0	0	0	0	0	1	0	0
Drassyllus.pusillus	0	1	0	0	0	0	0	3	1	0
Erigone.atra	1	0	5	0	5	1	1	1	4	0
Erigone.dentipalpis	0	0	3	0	5	0	3	4	4	0
Hahnia.nava	0	6	0	1	0	2	0	5	1	0
Haplodrassus.signifer	0	0	0	0	0	0	0	0	0	0
Tenuiphantes.tenius	0	0	0	0	0	0	0	0	0	0
Meioneta.affinis	1	4	0	2	0	0	0	4	0	0
Meioneta.rurestris	0	1	0	2	0	0	0	2	0	0
Mermessus.trilobatus	0	1	0	0	0	1	0	1	0	0
Micaria.pulicaria	0	0	0	0	0	0	0	0	0	0
Oedothorax.fuscus	2	1	118	1	54	28	37	7	81	18
Oedothorax.retusus	0	0	11	1	8	5	16	0	41	10
Ozyptila.simplex	0	1	1	11	2	7	2	2	1	7
Pachygnatha.clercki	1	0	4	0	2	0	1	0	11	1
Pachygnatha.degeeri	6	27	26	25	12	18	37	12	31	5
Pardosa.cf.agrestis	0	5	0	0	0	0	0	1	0	0
Pardosa.amentata	2	0	0	0	0	0	1	0	1	0
Pardosa.hortensis	0	0	0	0	0	0	0	0	0	0
Pardosa.lugubris	0	0	0	1	0	0	0	0	0	0
Pardosa.palustris	233	12	165	78	74	101	249	59	31	27
Pardosa.prativaga	2	1	21	14	11	8	5	3	5	0
Pardosa.pullata	2	88	12	33	48	30	13	38	71	32
Pelecopsis.parallela	1	0	14	1	2	2	3	7	0	1
Phrurolithus.festivus	0	0	0	1	0	0	0	1	0	0
Phrurolithus.minimus	0	0	0	0	0	0	0	0	0	0
Pirata.latitans	0	0	0	0	0	0	0	0	1	0
Pirata.piraticus	0	0	0	0	0	1	0	1	0	0
Pirata.uliginosus	0	0	0	1	1	0	0	0	1	0
Thanatus.striatus	0	0	0	0	0	0	0	0	0	0
Tiso.vagans	0	0	0	0	0	0	0	0	0	0
Trochosa.ruricola	33	11	42	17	13	10	26	27	40	2
Trochosa.spinipalpis	0	0	0	3	0	0	0	0	0	0
Trochosa.terricola	0	0	1	2	0	2	0	0	0	1
Walckenaeria.antica	0	0	0	0	0	0	0	0	0	0
Xerolycosa.miniata	0	0	0	4	0	0	1	8	0	0
Xysticus.acerbus	1	2	1	3	0	3	3	4	3	0
Xysticus.audax	0	1	0	0	1	0	0	0	0	0
Xysticus.cristatus	1	0	1	1	1	0	0	2	0	0
Xysticus.kochi	0	0	2	0	1	0	0	0	2	0
Zelotes.latreillei	0	0	0	0	0	0	0	1	0	0
Trachyzelotes.pedestris	0	1	0	0	0	0	0	0	0	1

plot	1-06a	1-07b	3-03a	3-04c	5-05b	5-06a	5-07a	5-07b	5-11a	5-11b	5-13b
Alopecosa.cuneata	19	2	3	26	16	11	53	19	33	15	13
Alopecosa.pulverulenta	0	0	0	0	0	0	0	0	0	0	0
Araeoncus.humilis	0	0	1	0	0	0	0	0	0	0	0
Arctosa.leopardus	0	8	7	0	0	0	0	0	1	0	0
Arctosa.lutetiana	0	0	0	0	0	0	0	0	0	0	0
Arctosa.perita	0	1	0	0	0	0	0	0	0	0	0
Aulonia.albimana	0	0	0	0	0	0	2	0	1	0	0
Bathyphantes.gracilis	0	0	0	0	0	0	0	0	0	0	0
Ceratinella.brevipes	0	0	6	0	0	0	1	0	1	0	0
Cnephalocotes.obscuru	0	0	0	0	0	0	0	0	0	0	0
Dendryphantes.rudis	0	0	0	0	0	0	0	0	0	0	0
Dicymbium.nigrum	0	1	0	0	0	0	0	0	0	0	0
Diplostyla.concolor	0	0	0	0	0	0	0	1	0	0	0
Drassyllus.lutetianus	1	1	0	0	1	0	0	0	0	0	0
Drassyllus.praeficus	0	0	0	0	1	2	0	0	0	0	0
Drassyllus.pusillus	0	0	1	0	0	9	0	1	0	1	0
Erigone.atra	1	4	10	0	0	0	3	7	2	0	1
Erigone.dentipalpis	4	2	7	0	1	0	4	37	2	5	0
Hahnia.nava	1	1	0	0	0	7	0	0	2	0	0
Haplodrassus.signifer	0	0	0	0	1	0	0	0	0	0	0
Tenuiphantes.tenius	0	0	1	0	0	0	0	0	0	0	0
Meioneta.affinis	0	0	2	2	2	1	1	4	0	0	1
Meioneta.rurestris	2	2	1	4	1	1	2	7	0	2	0
Mermessus.trilobatus	0	0	0	0	0	0	2	14	0	2	2
Micaria.pulicaria	0	0	0	0	1	0	0	0	0	0	0
Oedothorax.fuscus	0	44	49	1	0	0	1	5	0	0	3
Oedothorax.retusus	0	0	4	0	0	0	0	0	0	0	0
Ozyptila.simplex	4	1	0	2	3	1	0	16	1	1	1
Pachygnatha.clercki	0	0	5	0	0	0	0	0	0	0	0
Pachygnatha.degeeri	13	6	4	1	0	8	6	23	5	3	9
Pardosa.cf.agrestis	0	1	0	0	0	0	0	0	0	0	0
Pardosa.amentata	0	0	0	0	0	0	1	0	1	0	1
Pardosa.hortensis	0	0	0	0	0	0	0	0	0	0	0
Pardosa.lugubris	0	0	0	0	0	0	0	0	0	0	0
Pardosa.palustris	189	63	75	170	26	20	266	74	98	25	121
Pardosa.prativaga	2	33	6	2	2	0	2	2	1	0	1
Pardosa.pullata	19	8	15	15	59	55	2	0	30	0	26
Pelecopsis.parallela	0	0	6	2	1	0	0	1	0	2	0
Phrurolithus.festivus	0	0	0	0	0	0	0	0	0	0	0
Phrurolithus.minimus	0	0	0	0	0	0	0	0	0	0	0
Pirata.latitans	0	0	0	0	0	0	0	0	0	0	0
Pirata.piraticus	0	0	2	0	0	0	1	0	0	0	1
Pirata.uliginosus	0	0	3	0	0	0	0	1	0	0	0
Thanatus.striatus	0	0	0	0	0	1	0	0	0	0	0
Tiso.vagans	1	0	0	0	0	0	0	0	0	0	1
Trochosa.ruricola	3	12	41	19	15	15	15	13	3	7	3
Trochosa.spinipalpis	0	0	0	0	0	0	0	0	0	0	0
Trochosa.terricola	0	0	0	0	0	0	0	0	0	1	0
Walckenaeria.antica	0	0	0	0	1	0	0	0	0	0	0
Xerolycosa.miniata	3	0	0	3	0	4	3	1	0	3	0
Xysticus.acerbus	0	3	0	0	0	2	0	0	3	1	1
Xysticus.audax	0	1	1	0	0	0	0	1	0	0	0
Xysticus.cristatus	1	0	0	0	0	0	1	0	0	0	0
Xysticus.kochi	1	0	0	0	0	1	0	2	0	1	0
Zelotes.latreillei	0	0	0	0	0	0	0	0	0	0	0
Trachyzelotes.pedestris	0	0	0	0	0	3	0	0	0	0	0

5-13a	5-12a	5-10a	5-09a	5-08b	5-08a	5-03a	plot
23	35	48	6	55	0	1	***Alopecosa.cuneata***
0	0	0	0	0	0	0	***Alopecosa.pulverulenta***
0	0	0	0	0	0	0	***Araeoncus.humilis***
0	0	0	2	0	3	0	***Arctosa.leopardus***
0	1	0	0	0	0	0	***Arctosa.lutetiana***
0	0	0	0	0	0	0	***Arctosa.perita***
0	0	1	2	0	0	0	***Aulonia.albimana***
0	0	0	0	0	1	0	***Bathyphantes.gracilis***
0	3	1	2	2	0	0	***Ceratinella.brevipes***
0	0	0	0	0	0	0	***Cnephalocotes.obscuru***
0	0	1	0	0	0	0	***Dendryphantes.rudis***
0	0	0	0	0	1	0	***Dicymbium.nigrum***
0	0	0	0	0	0	0	***Diplostyla.concolor***
0	0	1	0	0	0	0	***Drassyllus.lutetianus***
0	0	0	0	0	0	0	***Drassyllus.praeficus***
1	0	3	0	0	1	0	***Drassyllus.pusillus***
0	0	0	0	0	0	1	***Erigone.atra***
2	0	1	1	2	1	2	***Erigone.dentipalpis***
0	0	0	0	0	0	2	***Hahnia.nava***
0	0	0	0	0	0	0	***Haplodrassus.signifer***
0	0	0	0	0	0	0	***Tenuiphantes.tenius***
8	1	7	1	0	0	0	***Meioneta.affinis***
0	1	0	5	0	0	0	***Meioneta.rurestris***
1	1	1	0	0	1	0	***Mermessus.trilobatus***
0	1	0	0	0	0	0	***Micaria.pulicaria***
0	18	1	2	0	8	4	***Oedothorax.fuscus***
1	2	1	1	0	10	1	***Oedothorax.retusus***
2	0	2	4	1	1	1	***Ozyptila.simplex***
0	0	0	0	0	1	0	***Pachygnatha.clercki***
3	23	5	8	12	15	36	***Pachygnatha.degeeri***
0	0	0	0	0	0	0	***Pardosa.cf.agrestis***
0	0	0	1	0	0	1	***Pardosa.amentata***
1	0	0	0	0	0	0	***Pardosa.hortensis***
0	0	0	0	0	0	0	***Pardosa.lugubris***
62	61	25	99	26	0	87	***Pardosa.palustris***
0	5	5	1	0	24	5	***Pardosa.prativaga***
0	25	54	27	33	28	0	***Pardosa.pullata***
0	2	24	2	1	2	8	***Pelecopsis.parallela***
0	0	1	0	0	0	0	***Phrurolithus.festivus***
0	0	2	0	0	0	0	***Phrurolithus.minimus***
0	0	0	0	0	0	0	***Pirata.latitans***
0	0	0	0	0	0	0	***Pirata.piraticus***
0	0	0	0	0	6	0	***Pirata.uliginosus***
0	0	0	0	0	0	0	***Thanatus.striatus***
0	0	0	0	0	1	0	***Tiso.vagans***
8	11	14	37	9	2	27	***Trochosa.ruricola***
0	0	0	0	0	0	0	***Trochosa.spinipalpis***
2	3	4	0	0	1	0	***Trochosa.terricola***
1	0	0	0	0	0	0	***Walckenaeria.antica***
17	1	0	0	3	0	0	***Xerolycosa.miniata***
0	0	0	1	0	0	2	***Xysticus.acerbus***
0	0	0	1	0	0	2	***Xysticus.audax***
0	0	0	0	0	3	0	***Xysticus.cristatus***
0	0	0	0	0	0	0	***Xysticus.kochi***
0	0	0	0	0	0	0	***Zelotes.latreillei***
0	0	0	0	0	0	0	***Trachyzelotes.pedestris***

APPENDIX D

Chapter 5: Müller, I.B. et al. (in prep.). Experiment(s) on the effect of traditional Experiment(s) on the effect of traditional flood irrigation on the availability of plant nutrients for Central European grassland species.

D. 1. Nutrient availability in mesocosms under three grassland species**.**

Tab. 1. Plant available nutrients (mean and SE) in the mesocosms with three different species before and after irrigation. Nutrient availability was determined with Plant Root Simulators™ (PRS; Western Agricultural Innovations, Saskatoon, Saskatchewan, Canada). Nutrient availability before and after irrigation was measured for 5 days and during irrigation for 1 day. Letters indicate significant difference in the nutrient availability between the different species before irrigation. Data in bold indicate statistical significance ($p \leq 0.05$) and bold italics indicate marginal significance ($p \leq 0.1$). Statistical significance was only tested for nutrient availability before versus after irrigation.

Macro-nutrients		**NO_3-N**	**NH_4-N**	**P**	**K**	**Ca**	**Mg**	**S**
	Irrigation	**µg·10 cm^{-2}**						
Centaurea jacea (a)	before	15.9 ± 3.34	**3.92 ± 0.67**	**6.9 ± 1.57**	18.13 ± 4.46	**1923.77 ± 92.22 b.c**	**249.31 ± 7.46 b.c**	**167.05 ± 27.77**
	during	27.06 ± 6.51	6.07 ± 0.58	7.09 ± 1.81	14.73 ± 3.85	2654.94 ± 178.65	315.78 ± 23.38	235.2 ± 43.08
	after	20.15 ± 2.98	**2.3 ± 0.21**	**1.46 ± 0.4**	21.57 ± 3.34	**1278.04 ± 180.45**	**184.76 ± 26.23**	**47.99 ± 14.7**
Polygonum periscaria (b)	before	32.67 ± 8.55	**5.22 ± 1.64**	***10.41 ± 5.36***	11.12 ± 2.78	**2376.07 ± 146.28 a.c**	**283.68 ± 13.05 a.c**	127.82 ± 18.15
	during	53.1 ± 16.81	4.1 ± 0.46	6.71 ± 1.78	7.15 ± 0.95	2504.67 ± 69.01	286.77 ± 4.67	204.92 ± 48.61
	after	28.22 ± 7.72	**1.8 ± 0.32**	***2.42 ± 0.37***	10.81 ± 2.66	**1552.03 ± 139.41**	**214.71 ± 14.85**	53.89 ± 15.22
Holcus lanatus (c)	before	13.78 ± 3.66	2.64 ± 0.89	5.91 ± 2.47	91.81 ± 40.19 ***a*.b**	1111.51 ± 212.84 **a.b**	162.86 ± 28.24 **a.b**	84.7 ± 30.79
	during	24.42 ± 5.3	5.98 ± 1.21	11.65 ± 2.61	34.3 ± 17.3	2555.63 ± 137.63	348.79 ± 16.45	517.93 ± 35.88
	after	30.88 ± 5.84	5.05 ± 2.72	5.12 ± 0.8	41.81 ± 11.62	1338.86 ± 67.82	192.27 ± 14.22	67.8 ± 10.66

Micro-nutrients			**Mn**	**Cu**	**Zn**	**B**
	Irrigation		**µg·10 cm^{-2}**			
Centaurea jacea (a)	before	***53.23 + 14.83 b***	**21.94 + 5.73 *b*.c**	**2.1 + 0.35 *b***	**5.58 + 0.66 b.c**	0.66 + 0.**16 b**.*c*
	during	199.94 + 22.57	56.72 + 7.43	4.64 + 0.48	9.46 + 1.04	0.96 + 0.15
	after	***21.12 + 6.17***	**6.79 + 1.58**	**0.98 + 0.33**	**1.5 + 0.27**	0.74 + 0.19
Polygonum periscaria (b)	before	**253.02 + 96.23 *a*.c**	**63.53 + 18.66 *a*.c**	***3.33 + 0.57 a*.c**	**9.18 + 1.38 a.c**	**1.3 + 0.21 a.c**
	during	231.92 + 39.12	67.49 + 8.62	10.93 + 2.26	14.04 + 2.19	1.59 + 0.34
	after	**19.15 + 4.39**	**5.6 + 2.22**	***1.52 + 0.38***	**1.96 + 0.36**	**0.61 + 0.08**
Holcus lanatus (c)	before	***10.74 + 4.4* a.b**	1.58 + 0.52 **a.b**	1.11 + 0.61 **b**	2.32 + 0.8 **a.b**	0.28 + 0.1 ***a*.b**
	during	249.68 + 22.36	41.85 + 5.41	14.53 + 1.67	20.02 + 2.29	1.88 + 0.38
	after	***14.82 + 2.71***	1.43 + 0.18	1.47 + 0.17	2.8 + 0.32	0.19 + 0.07

D. 2. Results of the statistical analysis of the nutrient availability (general and species-dependent) in the mesocosms.

Tab. 1. Analysis results of the nutrient availability before, during and after irrigation independent of the three test species (mean). ANOVA with a subsequent Tukey post-hoc test was performed when the assumption of homogeneity of variances was not violated (Levene's test from means). If homogeneity of variances was not given Friedman test with a subsequent Wilcoxon pairwise test was performed. Significant results ($p \leq 0.05$) are marked in bold; marginally significant results ($p \leq 0.1$) are marked in bold italics.

	ANOVA / Friedman test			**Tukey pairwise / Wilcoxon pairwise**		
General nutrient availability						
	F	**p**	**Chi2**	**before vs. during**	**during vs. after**	**before vs. after**
NO_3	4,71	**0.01**		**0.01**	0.56	0.13
NH_4	11,49	**< 0.001**		**0.04**	**< 0.001**	***0.06***
P	14,39	**< 0.001**		0.97	**< 0.001**	**< 0.001**
K	2.94	0.23		***0.05***	0.14	0.92
Ca		**< 0.001**	24.82	**< 0.001**	**< 0.01**	**< 0.001**
Mg	18,82	**< 0.001**		**< 0.01**	**< 0.001**	0.11
S		**< 0.001**	21.52	**< 0.001**	**< 0.001**	**< 0.01**
Fe		**< 0.001**	20.23	**< 0.001**	**< 0.001**	**< 0.01**
Mn		**< 0.001**	24.82	**< 0.001**	**< 0.001**	**< 0.01**
Cu		**< 0.001**	26.94	**< 0.001**	**< 0.001**	**0.03**
Zn		**< 0.001**	23.05	**< 0.01**	**< 0.001**	**< 0.001**
B		**< 0.001**	9.97	**< 0.01**	**< 0.001**	0.51

Tab. 2. Analysis results of the nutrient availability before, during and after irrigation depending on the three test species. ANOVA with a subsequent Tukey post-hoc test was performed when the assumption of homogeneity of variances was not violated (Levene’s test from means). If homogeneity of variances was not given Friedman test with a subsequent Wilcoxon pairwise test was performed. Significant results ($p \leq 0.05$) are marked in bold; marginally significant results ($p \leq 0.1$) are marked in bold italics.

	ANOVA / Friedman test			**Tukey pairwise / Wilcoxon pairwise**		
			Centaurea jacea			
	F	**p**	**Chi2**	**before vs. during**	**during vs. after**	**before vs. after**
NO_3	1,82	0,21		0,19	0,75	0,49
NH_4	19,40	**< 0.001**		**0,01**	**< 0.001**	***0,05***
P	5,67	**0,02**		0,99	**0.03**	**0.04**
K	3,68	***0,06***		0,40	***0.05***	0,39
Ca	15,20	**< 0.001**		0,03	**< 0.001**	***0,06***
Mg		**< 0.01**	10.33	***0,07***	**0.04**	**0.04**
S	24,20	**< 0.001**		***0.07***	**< 0.01**	**< 0.001**
Fe	34,77	**< 0.001**		**< 0.001**	**< 0.001**	0,37
Mn		**< 0.01**	10.33	**0,04**	**0,04**	***0,07***
Cu	36,86	**< 0.001**		**< 0.01**	**< 0.001**	**< 0.01**
Zn		**< 0.01**	10.33	***0.07***	**0.04**	**0.04**
B	0.96	0.41		0,40	0.61	0.92
			Polygonum persicaria			
	F	**p**	**Chi2**	**before vs. during**	**during vs. after**	**before vs. after**
NO_3	2.18	0.16		0.22	0.20	0.99
NH_4			9.33	0.44	**0.04**	**0.04**
P		**< 0.01**	10.33	0.44	**0.04**	**0.04**
K		0.56	1.33	1	0.23	0.32
Ca	25,40	**< 0.001**		0.88	**< 0.001**	**< 0.001**
Mg	17,19	**< 0.001**		0.98	**< 0.01**	**< 0.01**
S		***0.07***	5.33	***0.07***	***0.07***	0.23
Fe		**< 0.01**	9	1	**0.04**	**0.04**
Mn		**< 0.01**	9.33	0.84	**0.04**	**0.04**
Cu		**< 0.01**	10.33	**0.04**	**0.04**	0.10
Zn		**< 0.01**	9.33	0.32	**0.04**	**0.04**
B	4.21	**0.04**		0.67	**0.04**	0.16

	ANOVA / Friedman test			**Tukey pairwise / Wilcoxon pairwise**		
	Holcus lanatus					
	F	**p**	**Chi2**	**before vs. during**	**during vs. after**	**before vs. after**
NO_3	3.43	***0.08***		0.29	0.60	***0.07***
NH_4	2.51	0.14		0.12	0.46	0.60
P	8,45	**0.01**		**0.01**	**0.02**	0.94
K	1.57	0.27		0.29	0.97	0.38
Ca	32,28	**< 0.001**		**< 0.001**	**< 0.001**	0.49
Mg	22,54	**< 0.001**		**< 0.001**	**< 0.01**	0.60
S	177.30	**< 0.001**		**< 0.001**	**< 0.001**	0.81
Fe	142,50	**< 0.001**		**< 0.001**	**< 0.001**	***0.09***
Mn		**0.02**	7,6	***0.09***	***0.09***	1
Cu		**< 0.01**	8,4	***0.09***	***0.09***	0.63
Zn		**0.02**	7,6	***0.09***	***0.09***	0.45
B		**0.02**	7.6	***0.09***	***0.09***	0.63

STATUS AND AUTHOR CONTRIBUTIONS OF THE PUBLICATIONS INCLUDED IN THE THESIS

Chapter 2 : Müller, I.B., Buhk, C., Alt, M., Entling, M.H., Schirmel, J. (2015). Plant functional shifts in Central European grassland under traditional flood irrigation. *Applied Vegetation Science.*

IBM, MHE, JS and MA conceived and designed the study. IBM performed the species sampling. DL helped with the study site selection and species determination. IBM analyzed the data and wrote the manuscript. CB, JS, MHE provided statistical and editorial advice.

Chapter 3: Müller, I.B., Buhk, C., Lange, D., Entling, M.H., Schirmel, J. (2016). Contrasting effects of irrigation and fertilization on plant diversity in hay meadows. *Basic and Applied Ecology.*

IBM, MHE and JS conceived and designed the study. IBM performed the species sampling. DL helped with the study site selection and species determination. IBM analyzed the data and wrote the manuscript. CB, JS, MHE provided statistical and editorial advice.

Chapter 4: Schirmel, J, Alt, M, Müller, IB, Entling, MH (2014) Effects of Traditional Flood Irrigation on Invertebrates in Lowland Meadows. *PLoS ONE 9(10).*

JS, MHE and MA conceived and designed the study. IBM assisted the species sampling. JS analyzed the data and wrote the manuscript. JS, MHE and IBM provided statistical and editorial advice.

Chapter 5: Müller, I.B., Buhk, C.B., Diehl, D., Jungkunst, H.F. (to be submitted). Experiment(s) on the effect of traditional flood irrigation on the availability of plant nutrients for Central European grassland species. Journal for submission: *Agriculture, Ecosystems & Environment.*

IBM, CB, DD and HFJ conceived and designed the study. IBM installed the experimental setups and performed the measurements. IBM analyzed the data and wrote the manuscript. CB, HFJ and DD provided statistical and editorial advice.

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10/2006 - 03/2011	**Studium:** Biologie und Englisch für das Lehramt an Realschulen, Universität Koblenz-Landau, Landau
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06/2011 - 09/2012	**Promotionseignungsstudium im Fach Biologie**, Universität Koblenz-Landau, Landau
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Weitere Arbeitserfahrung

04/2011 – 02/2012	**Förderlehrkaft** im Angestelltenverhältnis, IGS Rülzheim, Rülzheim
2011 - 2013	**Betreuung** botanischer und vegetationskundlicher Exkursionen, Universität Koblenz-Landau und Volkshochschule Inzigkofen
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2011 - 2014	**Wissenschaftliche Hilfskraft** in diversen botanischen Praktika für Lehramtsstudierende, Universität Koblenz-Landau, Landau
6/2012	**Workshop** „Pollination Ecology“, Royal Botanic Gardens Kew, London (UK)
01/2014-03/2014	**Gastwissenschaftlerin** am Max Planck Institut für Biogeochemie (Department Biogeochemische Prozesse), Jena
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Sprachkenntnisse

Englisch	sehr gute Kenntnisse in Wort und Schrift (1. Staatsexamen)
Französisch	Grundkenntnisse

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Böhl-Iggelheim, den _________________ ______________________

Isabell Müller

Declaration according to §8 of the Promotionsordnung des Fachbereichs 7: Natur- und Umweltwissenschaften der Universität Koblenz-Landau, Campus Landau vom 14.06.2013

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