



Contrasting effects of irrigation and fertilization on plant diversity in hay meadows

Isabell B. Müller*, Constanze Buhk, Dagmar Lange, Martin H. Entling,
Jens Schirmel

University of Koblenz-Landau, Institute for Environmental Science, Fortstraße 7, D-76829 Landau, Germany

Received 27 July 2015; accepted 28 April 2016
Available online 6 May 2016

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.

Zusammenfassung

Extensive Grünlandbewirtschaftung liefert einen wesentlichen Beitrag zum Erhalt der Biodiversität. Die Vereinbarkeit von Biodiversität und hohen landwirtschaftlichen Erträgen stellt jedoch eine große Herausforderung dar. Traditionelle Wiesenbewässerung war eine weitverbreitete Bewirtschaftungsform zur Steigerung des Heuertrags. Als Folge der Intensivierung der Grünlandnutzung wurde die Wiesenbewässerung jedoch vielerorts aufgegeben. In unserer Feldstudie untersuchten wir den Langzeiteinfluss von traditioneller Wiesenbewässerung in Kombination mit Düngung und Biomasseproduktion auf die Phytodiversität. Unsere Ergebnisse zeigten einen überwiegend positiven Einfluss traditioneller Wiesenbewässerung auf die pflanzliche Alpha-Diversität (Simpson-Diversität und Äquität) und Beta-Diversität (*heterogeneity of multivariate dispersions*). Die Stärke und Signifikanz der Effekte unterschied sich jedoch zwischen den beiden Untersuchungsjahren, was möglicherweise an den verschiedenen Witterungsbedingungen lag. Im Hinblick auf die Artenanzahl konnten wir keinen Effekt der Bewässerung feststellen, es zeigte sich aber ein negativer Effekt der Menge an Stickstoffdünger. Weiterhin zeigten sich sowohl unimodale

*Corresponding author. Tel.: +49 06341 280 31521.
E-mail address: rudolph@uni-landau.de (I.B. Müller).

(Artenanzahl und Simpson-Diversität) als auch lineare (Äquität) Zusammenhänge zwischen der pflanzlichen Alpha-Diversität und Biomasse. Die überwiegend höhere pflanzliche Alpha- und Beta-Diversität in bewässerten Wiesen resultiert vermutlich aus der jährlich wiederkehrenden künstlichen Bewässerung, die sowohl auf Flächen- als auch auf Landschaftsebene heterogen ist. Diese Ergebnisse zeigen dass traditionelle Wiesenbewässerung mit dem Erhalt der Biodiversität in Wirtschaftsgrünland vereinbar ist. Deutlich wertvoller für den Naturschutz könnten jedoch diversifizierte Bewässerungsmethoden sein, die auch länger andauernde Überflutung zur Förderung stärker hygrophiler Vegetationstypen umfassen.

© 2016 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Keywords: Flood irrigation; Grassland; Meadow irrigation; Phytodiversity; Plant biomass

Introduction

Semi-natural grasslands are key habitats for biodiversity conservation (Poschold & Wallis DeVries 2002; Baur et al. 2006) but have declined due to management intensification and abandonment within the past centuries (Poschold, Bakker, & Kahmen 2005, Wesche, Krause, Culmsee, & Leuschner 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 2003; Kleijn et al. 2009). However, it is challenging to combine biodiversity conservation with efficient agricultural land-use (Tschardt 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 (Müller 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, Pellet, Buri, & Arlettaz 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; Riedener, Rusterholz, & Baur 2013, Leibundgut & Kohn 2014a). In Germany, irrigation history can be traced back

to the 12th and 13th century (Endriss 1951) 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, Dwyer, Andrey, & Arlettaz 2016): 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, Amiaud, Mignolet, & Plantureux 2012 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 (Hoppe 2012; Riedener et al. 2013) and affecting plant diversity (Riedener et al. 2013; Andrey, Humbert, Pernollet, & Arlettaz 2014) as well as functional composition (Müller et al. 2016).

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 2–3 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 ($n_{\text{non-irrigated/unfertilized}} = 9$, $n_{\text{non-irrigated/fertilized}} = 4$, $n_{\text{irrigated/unfertilized}} = 8$, $n_{\text{irrigated/fertilized}} = 12$). 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 to 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 m × 3 m, $n_{\text{total}} = 99$) 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 cm × 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, Ieno, Walker, Saveliev, & Smith 2009). Tests for

significance were done with permutational ANOVA (command ‘PermTest’ in R library ‘pgrimmess’; 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

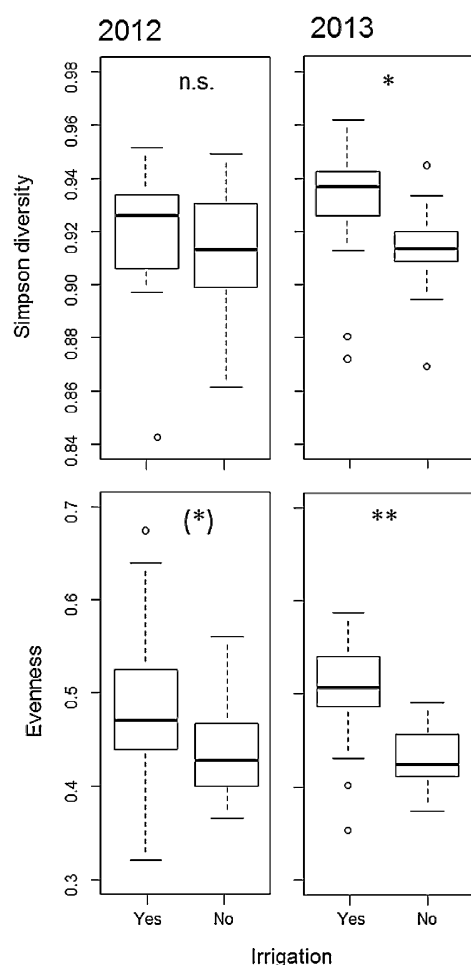


Fig. 1. Effects of meadow irrigation on Simpson diversity and Evenness of plants in 2012 and 2013. Significance was tested with linear models and permutational ANOVA (see Table 1). n.s. not significant, (*) $P < 0.1$, * $P < 0.05$, ** $P < 0.01$.

Table 1. Relation of plant alpha diversity to irrigation (yes/no), fertilization ($\text{N ha}^{-1} \text{ year}^{-1}$), and aboveground biomass (g/m^2 ; only in 2013). Significance of explanatory variables was tested with permutational ANOVA.

Response	Explanatory variables	Estimate	<i>p</i>
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	<i>0.056</i>
	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	<i>0.056</i>
	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

Significant ($p < 0.05$) results are marked in bold and marginally significant ($p < 0.1$) are given in italics.

irrigation but decreased with increasing amount of fertilization in both years (Table 1, Fig. 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 (Table 1). Both species richness and Simpson diversity showed a hump-shaped response and peaked at intermediate biomass values (Fig. 3A and B), whereas Evenness decreased monotonously with increasing biomass (Fig. 3C).

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 ($F_{1,31} = 5.2$, $P = 0.029$) (Fig. 4a). In contrast, mean distances to the centroid did not differ significantly between irrigated and non-irrigated meadows in 2013 ($F_{1,30} = 1.6$, $P = 0.213$) (Fig. 4b).

Unexpectedly, fertilization had no significant influence on plant beta diversity. In both years the mean distances to the

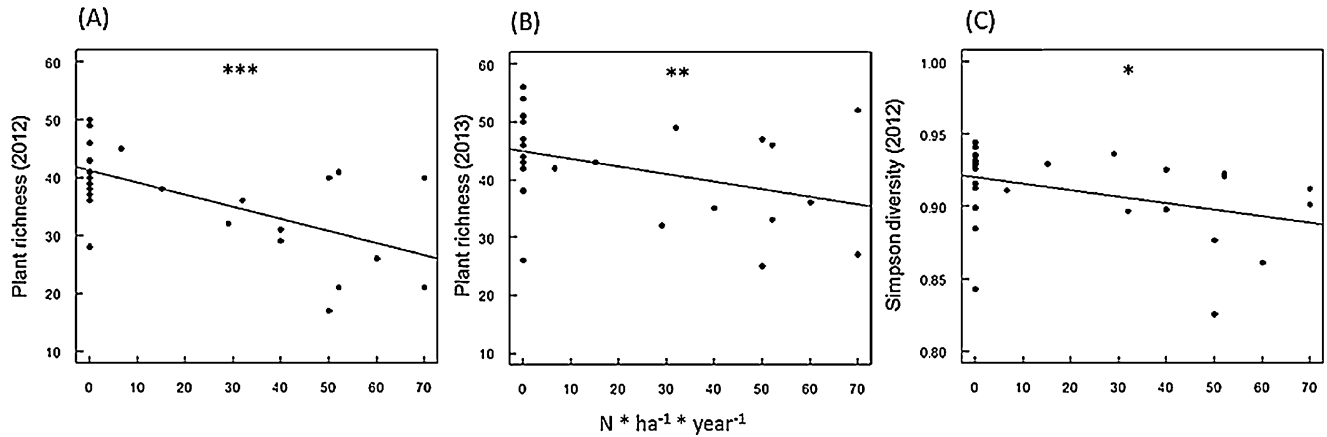


Fig. 2. Negative effects of fertilization ($\text{N ha}^{-1} \text{ year}^{-1}$) on plant species richness in (A) 2012 and (B) 2013 and on (C) Simpson diversity in 2012 in traditional irrigated meadows. Significance was tested with linear models and ANOVA or permutational ANOVA (see Table 1). * $P <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

centroid did not significantly differ between fertilized and unfertilized meadows (2012: $F_{1,31} = 1.8$, $P = 0.190$; 2013: $F_{1,31} = 1.2$, $P = 0.281$) (Fig. 5).

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 et al. 2013; Müller et al. 2016). 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

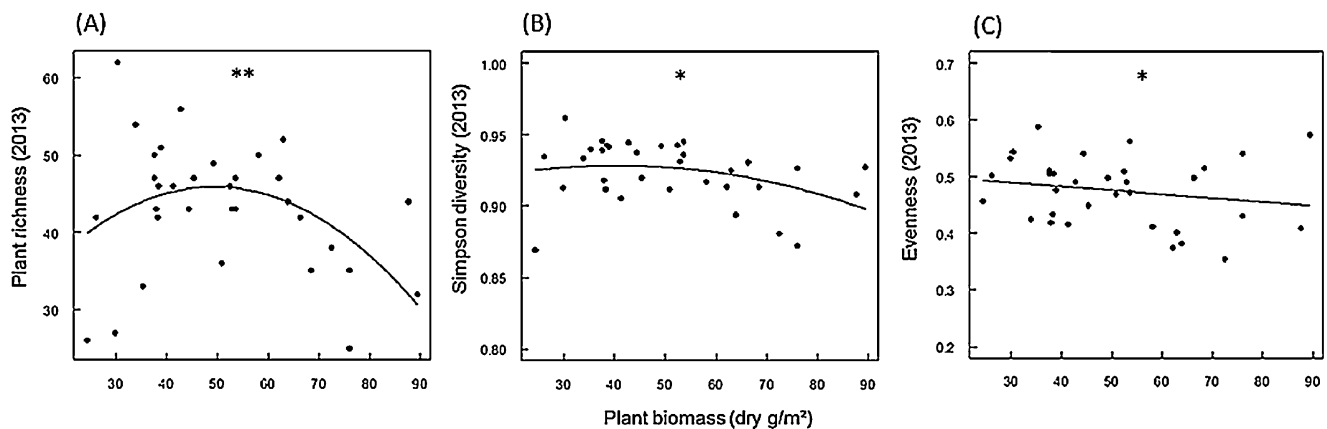


Fig. 3. Relationships between plant biomass and (A) plant species richness, (B) Simpson diversity and (C) Evenness in 2013 in traditional irrigated meadows. Significance was tested with linear models and ANOVA or permutational ANOVA (see Table 1). * $P < 0.05$, ** $P < 0.001$.

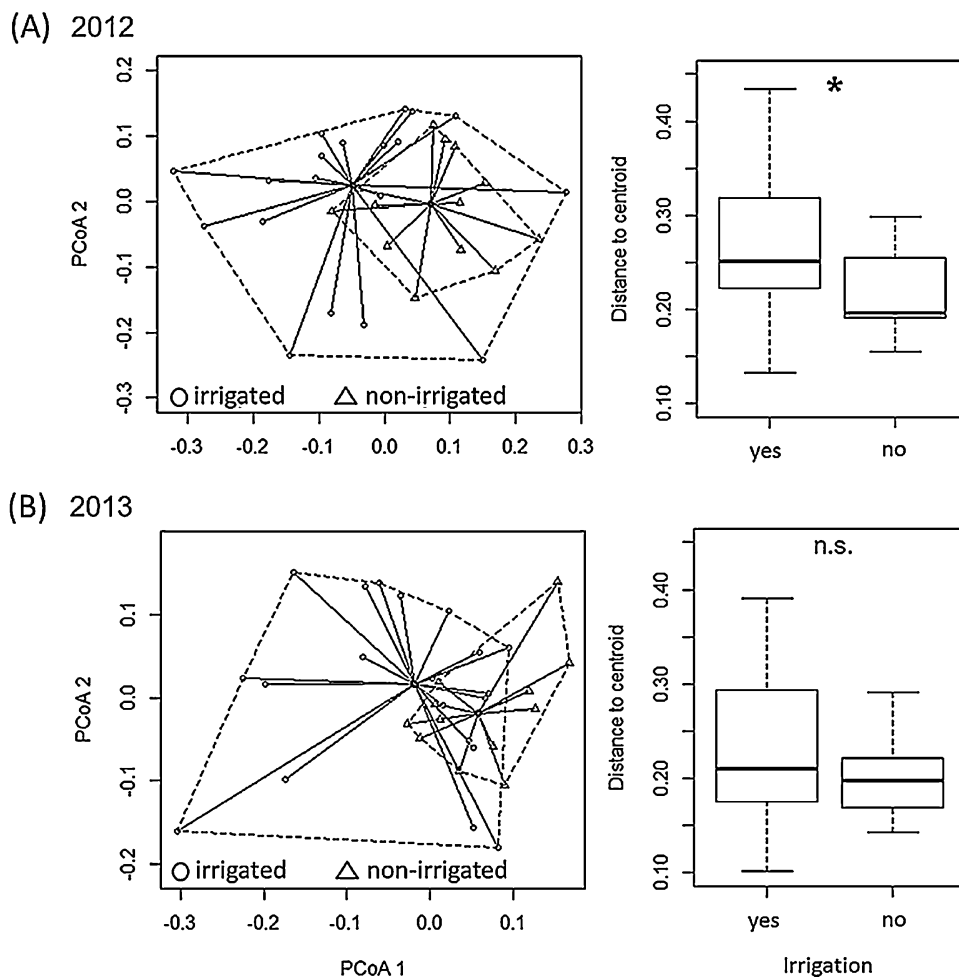


Fig. 4. Plant beta diversity (mean distance to centroid) of irrigated and non-irrigated meadows in (A) 2012 and (B) 2013. Differences were tested with homogeneity of multivariate dispersions (see text). n.s. not significant, $*P < 0.05$.

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 (Pollock, Naiman, & Hanley 1998). The long-term impact of irrigation on the plant species composition is discussed in Müller et al. (2016). 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 et al. 2009; Gaujour et al. 2012 and references

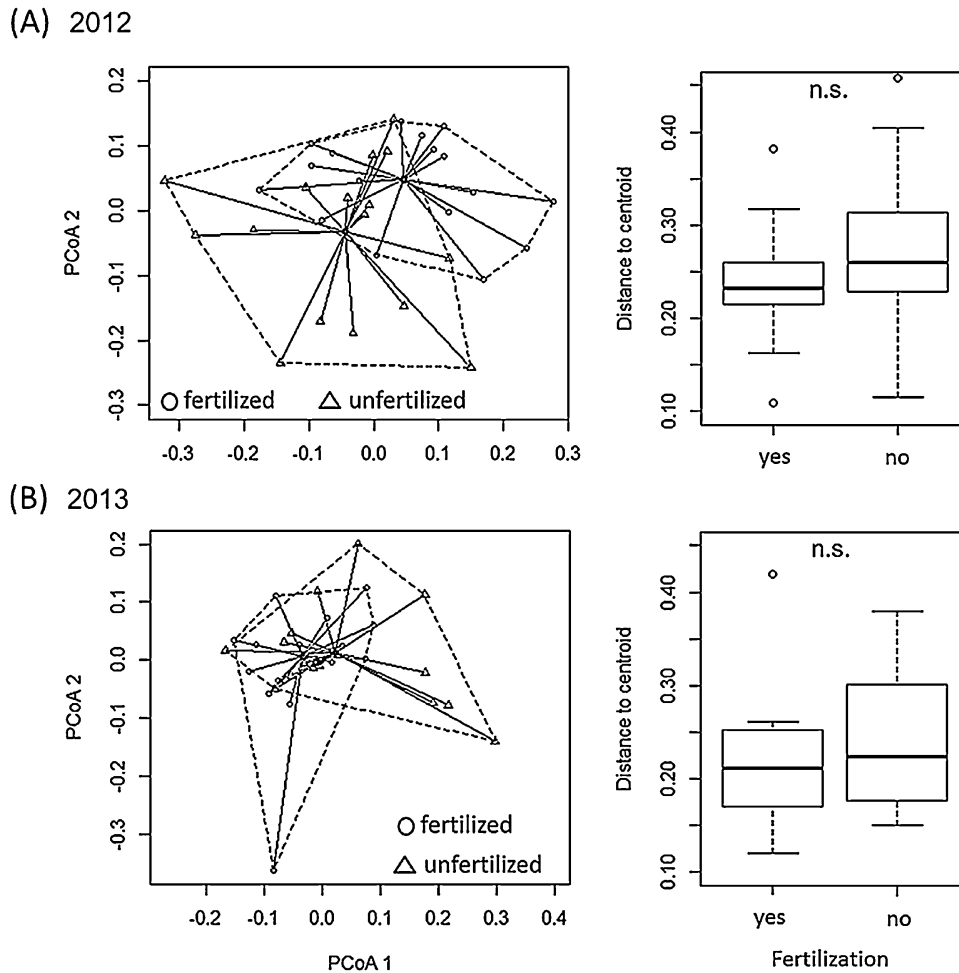


Fig. 5. Plant beta diversity (mean distance to centroid) of fertilized and unfertilized meadows in (A) 2102 and (B) 2013. Differences were tested with homogeneity of multivariate dispersions (see text). n.s. not significant.

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. 2016). 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 et al. 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 Thorhallsdottir (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, Olf, Willems, & Zobel 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, Alt, Rudolph, & Entling 2014). Moreover, irrigation may be beneficial for farmers by improving both biomass production (Cook, Cutting, Buhler, & Cummings 2004; Stearne & Cook 2014) 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 hydrophilic plant communities.

Acknowledgements

This work has been carried out in the framework of the research initiative AufLand, financed by the ‘Ministerium für Bildung, Wissenschaft, Weiterbildung und Kultur Rheinland-Pfalz’. The permission to carry out our studies in the Queich meadows was issued by the SGD Süd. We kindly thank the

landowners for the permission to work in their meadows and for the provision of information about the management. We thank Clarissa Schmitt, Nina Kessler and Tanja Siebert for the assistance with the biomass sampling. Two reviewers provided valuable comments on an earlier version of this manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2016.04.008>.

References

- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, *9*(6), 683–693.
- Andrey, A., Humbert, J.-Y., Pernollet, C., & Arlettaz, R. (2014). Experimental evidence for the immediate impact of fertilization and irrigation upon the plant and invertebrate communities of mountain grasslands. *Ecology and Evolution*, *4*(12), 2610–2623.
- Bakker, J., Olf, H., Willems, J., & Zobel, M. (1996). Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science*, *7*(2), 147–156.
- Baur, B., Cremene, C., Groza, G., Rakosy, L., Schileiko, A. A., Baur, A., et al. (2006). Effects of abandonment of subalpine hay meadows on plant and invertebrate diversity in Transylvania, Romania. *Biological Conservation*, *132*(2), 261–273.
- Briem, E., & Geiger, M. (2008). Das Fließgewässer Queich. In M. Geiger (Ed.), *Haardt, Weinstraße und Queichtal: Ein Geoführer* (pp. 114–116). Neustadt/Weinstraße: Pollichia.
- Cook, H. F., Cutting, R. L., Buhler, W., & Cummings, I. P. (2004). Productivity and soil nutrient relations of bedwork watermeadows in southern England. *Agriculture, Ecosystems & Environment*, *102*(1), 61–79.
- Dienstleistungszentrum Ländlicher Raum RLP. Agrarmeteorologie Rheinland-Pfalz. <http://www.am-rlp.de> Accessed 22.05.15.
- Dierschke, H., & Briemle, G. (2008). *Kulturgrasland: Wiesen, Weiden und verwandte Staudenfluren; 20 Tab. Ökologie Botanik*. Stuttgart: Ulmer.
- Endriss, G. (1951). Die künstliche Bewässerung des Schwarzwaldes und der angrenzenden Gebiete. *Berichte der Naturforschenden Gesellschaft Freiburg*, *4*, 1.
- Fiedler, K.-H. (1965). *Die Wiesenbewässerung im Saarland und in der Pfalz*. Saarbrücken, DE: Philosophische Fakultät der Universität des Saarlandes.
- Gaujour, E., Amiaud, B., Mignolet, C., & Plantureux, S. (2012). Factors and processes affecting plant biodiversity in permanent grasslands. A review. *Agronomy for Sustainable Development*, *32*(1), 133–160.
- Grime, J. P. (1973). Competitive exclusion in herbaceous vegetation. *Nature*, *242*, 344–347.

- Guo, Q. (2007). The diversity-biomass-productivity relationships in grassland management and restoration. *Basic and Applied Ecology*, 8(3), 199–208.
- Harpole, W. S., & Tilman, D. (2007). Grassland species loss resulting from reduced niche dimension. *Nature*, 446(7137), 791–793.
- Hassler, D. (Ed.). (1995). *Wässerwiesen: Geschichte, Technik und Ökologie der bewässerten Wiesen, Bäche und Gräben in Kraichgau, Hardt und Bruhrain; ein Gemeinschaftsprojekt des Landesnaturschutzverbandes Baden-Württemberg* (Vol. 87) Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg. Ubstadt-Weiher: Verl. Regionalkultur.
- Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science (New York, NY)*, 324(5927), 636–638.
- Hopkins, A., & Holz, B. (2006). Grassland for agriculture and nature conservation: Production, quality and multifunctionality. *Agronomy Research*, 3–20.
- Hoppe, A. (2012). *Die Europäische Wasserrahmenrichtlinie und historische Wasserbauten: Wege zur Erhaltung baulicher Anlagen bei Fließgewässerrenaturierungen; Abschlussbericht*. Hannover: Niedersächsischer Heimatbund.
- Humbert, J.-Y., Pellet, J., Buri, P., & Arlettaz, R. (2012). Does delaying the first mowing date benefit biodiversity in meadowland? *Environmental Evidence*, 1(1), 9.
- Humbert, J.-Y., Dwyer, J., Andrey, A., & Arlettaz, R. (2016). Impacts of nitrogen addition on plant biodiversity in mountain grasslands depend on dose, application duration and climate: A systematic review. *Global Change Biology*, 22, 110–120.
- Isselstein, J., Jeangros, B., & Pavlu, V. (2005). Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe – A review. *Agronomy Research*, 3, 139–151.
- Jongman, R. (2002). Homogenisation and fragmentation of the European landscape: Ecological consequences and solutions. *Landscape and Urban Planning*, 58(2–4), 211–221.
- Kleijn, D., & Sutherland, W. J. (2003). How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, 40(6), 947–969.
- Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E. D., Clough, Y., et al. (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings. Biological Sciences/The Royal Society*, 276(1658), 903–909.
- Lamb, E. G. (2008). Direct and indirect control of grassland community structure by litter, resources, and biomass. *Ecology*, 89(1), 216–225.
- Leibundgut, C. (2004). Historical meadow irrigation in Europe – A basis for agricultural development. In *The Basis of Civilization – Water Science? Proceedings of the UNESCO/IAI-IS/IWHA symposium* (pp. 77–87). IAI IS Publ 286.
- Leibundgut, C., & Kohn, I. (2014a). European traditional irrigation in transition Part I: Irrigation in times past – A historic land use practice across Europe. *Irrigation and Drainage*, 63(3), 273–293.
- Leibundgut, C., & Kohn, I. (2014b). European traditional irrigation in transition Part II: Traditional irrigation in our time – Decline, rediscovery and restoration perspectives. *Irrigation and Drainage*, 63(3), 294–314.
- Mittelbach, G. G., Steiner, C. F., Scheiner, S. M., Gross, K. L., Reynolds, H. L., Waide, R. B., et al. (2001). What is the observed relationship between species richness and productivity? *Ecology*, 82(9), 2381–2396.
- Müller, I. B., Buhk, C., Alt, M., Entling, M. H., Schirmel, J., & Hölzel, N. (2016). Plant functional shifts in Central European grassland under traditional flood irrigation. *Applied Vegetation Science*, 19(1), 122–131.
- Muller, S. (2002). Appropriate agricultural management practices required to ensure conservation and biodiversity of environmentally sensitive grassland sites designated under Natura 2000. *Agriculture, Ecosystems & Environment*, 89(3), 261–266.
- Giraudoux, P. (2014). *pgirmess: Data analysis in ecology. R package version 1.5.9*. <http://CRAN.R-project.org/package=pgirmess>
- Pollock, M. M., Naiman, R. J., & Hanley, T. A. (1998). Plant species richness in Riparian wetlands – A test of biodiversity theory. *Ecology*, 79(1), 94.
- Poschlod, P., Bakker, J. P., & Kahmen, S. (2005). Changing land use and its impact on biodiversity. *Basic and Applied Ecology*, 6(2), 93–98.
- Poschlod, P., & Wallis DeVries, M. F. (2002). The historical and socioeconomic perspective of calcareous grasslands-lessons from the distant and recent past. *Biological Conservation*, 104(3), 361–376.
- Rajaniemi, T. K. (2003). Explaining productivity–diversity relationships in plants. *Oikos*, 101(3), 449–457.
- Rees, M., & Brown, V. K. (1992). Interactions between invertebrate herbivores and plant competition. *Journal of Ecology*, 80, 353–360.
- Riedener, E., Rusterholz, H.-P., & Baur, B. (2013). Effects of different irrigation systems on the biodiversity of species-rich hay meadows. *Agriculture, Ecosystems & Environment*, 164, 62–69.
- Schellberg, S. (2005). Meadow irrigation in the federal state Baden-Württemberg. Portrayal of a nearly forgotten land use system. In *Integrated Land and Water Resources Management in History*. pp. 123–131. Sonderband 2: Schriften der DWhG.
- Schirmel, J., Alt, M., Rudolph, I., & Entling, M. H. (2014). Effects of traditional flood irrigation on invertebrates in lowland meadows. *PLOS ONE*, 9(10), e110854.
- Stampfli, A., & Zeiter, M. (2004). Plant regeneration directs changes in grassland composition after extreme drought: A 13-year study in southern Switzerland. *Journal of Ecology*, 92, 568–576.
- Stearne, K., & Cook, H. (2014). Water meadow management in Wessex: Dynamics of change from 1800 to the present day. *Landscape Research*, 40, 377–395.
- Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., et al. (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, 102(12), 4387–4392.
- Thorhallsdottir, T. E. (1990). The dynamics of a grassland community: A simultaneous investigation of spatial and temporal heterogeneity at various scales. *Journal of Ecology*, 78(4), 884.
- Tilman, D. (1982). *Resource competition and community structure*. Monographs in population biology (Vol. 17) Princeton, NJ: Princeton University Press.
- Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., et al. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation*, 151(1), 53–59.

- Waldhardt, R. (2003). Floristic diversity at the habitat scale in agricultural landscapes of Central Europe – Summary, conclusions and perspectives. *Agriculture, Ecosystems & Environment*, 98(1–3), 79–85.
- Wesche, K., Krause, B., Culmsee, H., & Leuschner, C. (2012). Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants. *Biological Conservation*, 150(1), 76–85.
- Wisskirchen, R., & Haeupler, H. (1998). *Standardliste der Farn- und Blütenpflanzen Deutschlands: Mit Chromosomenatlas von Focke Albers ([1. Aufl.]). Die Farn- und Blütenpflanzen Deutschlands: /hrsg. vom BN, Bundesamt für Naturschutz; 1. Stuttgart: Eugen Ulmer.*
- Zuur, A. F., Ieno, I. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. pp. 574. Berlin, Heidelberg: Springer.

Available online at www.sciencedirect.com

ScienceDirect