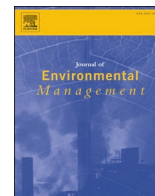




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Research article

Effects of fertilization and irrigation on vascular plant species richness, functional composition and yield in mountain grasslands

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ABSTRACT

Land-use intensification is a major threat to biodiversity in agricultural grasslands and fertilization is one of the main drivers. The effects of fertilization on biodiversity and plant functional composition (community-weighted mean traits and mean ecological indicator values) are well studied in lowland regions, but have received less attention in mountain grasslands. Moreover, in inner-alpine dry valleys, fertilizer is often applied in combination with irrigation, and irrigation effects are less well known. We experimentally tested the effects of fertilization and irrigation on vascular plant species richness and the functional composition of mountain grasslands in the Swiss Alps. After five years, fertilization increased yield but the relationship was quadratic with maximum yield reached at intermediate fertilizer levels (58 kg N ha⁻¹ year⁻¹). The species richness of all vascular plants and forbs decreased, on average, by 6 and 5 species respectively, per 50 kg N of extra fertilizer (ha⁻¹ year⁻¹) applied. Fertilization also favored fast-growing plants (increased mean specific leaf area) and plants typically found in productive environments (increased mean indicator values for soil productivity and moisture). In contrast, we found no effects of irrigation on plant community composition, which suggests that irrigation does not affect vascular plant diversity to the same extent as fertilization in these mesic mountain hay meadows, at least in the mid-term. Our finding that maximum yield can be achieved at intermediate fertilizer levels is very important from an applied, agronomical and conservation point of view. It suggests that without loss of yield, farming costs and at the same time environmental pollution and negative effects on biodiversity can be reduced by applying less fertilizer. We therefore recommend maintaining non-intensive land use and keeping fertilizer inputs as low as possible to maintain the high plant diversity of mountain grasslands.

Credit author statement

Raphaël Arlettaz and Jean-Yves Humbert conceived and designed the experiment and raised funds. Steffen Boch, Yasemin Kurtogullari, Malie Lessard-Therrien and Nora Simone Rieder gathered field data. Steffen Boch, Yasemin Kurtogullari, Gerard Martínez De León and Jean-Yves Humbert analyzed the data. Steffen Boch wrote the initial draft and all other authors commented on the manuscript. The manuscript has been spell and grammar checked by Eric Allan.

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1. Introduction

Grasslands cover wide areas of mountainous ecosystems in the Palaearctic, with cultural landscapes representing rich biodiversity hotspots, in particular in European massifs such as the Alps (Dengler

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et al., 2020). In Switzerland, grasslands cover about 30% of the total land area and the long history of traditional land-use systems has shaped their species diversity and composition (Boch et al., 2020).

Today, the major drivers of habitat degradation and loss of semi-natural grasslands are land-use abandonment and intensification, which are causing a general decline in biodiversity and an increase in the number of threatened species (Dengler et al., 2020). As temperate semi-natural grasslands depend on continuous farming, the abandonment and subsequent encroachment by woody vegetation leads to a loss of habitat quality and a decline of specialist and threatened species (Valkó et al., 2018; Boch et al., 2019a). Many grasslands have been intensified over the past decades to increase their productivity. For example, traditionally used grasslands have been largely replaced by fertilized grasslands, which can be mown frequently or grazed with high stocking densities (Boch et al., 2020). This land-use intensification is decreasing the biodiversity and alters species assemblages, leading to homogenization of grassland communities and reduced ecosystem multifunctionality (Allan et al., 2014; Hautier et al., 2018; Schirpke et al., 2020). While the effects of land-use intensification have been well studied in lowland regions, mountain grasslands have received less attention (Humbert et al., 2016).

With the aim to increase yield in dry agricultural regions of Europe, irrigation is another important aspect of grassland intensification, even outside the Mediterranean. Nowadays, in inner-alpine dry valleys, such as the Valais in Switzerland, hay meadows are often irrigated via aerial sprinklers. This can cause strong compositional changes and the loss of specialist species, especially in xeric vegetation types, because irrigation increases biomass production of fast-growing, mesophilous plant species which can outcompete low-statured and drought adapted species (Volkart, 2008). However, the impacts of irrigation on plant species richness have rarely been studied, especially so in mesic mountain grasslands (but see Riedener et al., 2013, 2014; and for short- and mid-term effects on vascular plant composition and bryophytes from the same experimental sites as this study: Andrey et al., 2014; Lessard-Therrien et al., 2017; Boch et al., 2018).

As climate-change projections for Switzerland suggest an increasing ambient temperature in all seasons and reduced precipitation in summer, with the strongest changes in the Southern Alps (Henne et al., 2018), irrigation might become even more important and widespread. This means that it is critical to better understand the long-term effects of irrigation on biodiversity and community composition.

Species richness is the most commonly used diversity measure in grassland studies. However, it does not capture different responses of functional plant groups to land use because species identity is not considered. Plant functional groups can be defined according to several morphological or physiological characteristics. Among herbaceous plant species, forbs, grasses and legumes are most commonly distinguished. However, classifying species into functional groups may be too simplistic and may ignore important trait variation. Functional response traits can predict shifts in plant species composition along environmental gradients and with changing land use. Such functional traits represent morpho-physio-phenological plant characteristics and are, for example, related to resource acquisition, growth and competition. As community-weighted means of these functional response traits provide more mechanistic insights into local vegetation responses, they are widely used in ecological studies (e.g. Pfestorf et al., 2013; Busch et al., 2019; Boeddinghaus et al., 2019). For example, mean specific leaf area (SLA) and leaf dry matter content (LDMC) are related to fertilization and resource utilization (Pfestorf et al., 2013), and might therefore mirror changes in soil fertility or water availability. In addition, the “leaf economics spectrum” (Wright, 2004) distinguishes fast-growing species with high SLA and low LDMC, which are adapted to high resource conditions, from slow growing species with low SLA and high LDMC (Westoby and Wright, 2006; Lienin and Kleyer, 2011).

Ecological indicator values aim to quantify the environmental niche of plant species on an ordinal scale and therefore can also be used to

visualize shifts in community composition (Ellenberg et al., 2001). Averaging the indicator values over all species occurring in a plot, while taking the species abundances into account (cover-weighted mean indicator values), can provide information on the environmental conditions of a site. Similar to functional response traits, ecological indicator values are widely used to characterize site conditions and temporal changes in vegetation plots (Diekmann, 2003; Boch et al., 2019b).

In this five-years experimental study from the Swiss Alps, we investigated the response of yield (plant biomass production), vascular plant species richness and functional composition to different intensities of slurry fertilization and sprinkler irrigation. Our main questions were:

- (1) How are yield and vascular plant species richness affected by fertilization and irrigation in mountain hay meadows?
- (2) Do fertilization and irrigation cause a shift in plant functional composition, as indicated by community-weighted mean traits and mean ecological indicator values?

2. Methods

2.1. Study sites

Our study area is located in the inner Alps (Valais, SW Switzerland). This region is characterized by a continental climate. In 2010, eleven traditionally managed meadows were selected, covering an elevational gradient from 880 to 1770 m above sea level (Tab. A1). Mean annual temperature and precipitation in the study area ranged from 4.2 to 9.4 °C and 600–750 mm, respectively (Boch et al., 2018). All meadows were at least 4000 m² in size, had received no or very low levels of fertilizer (only solid manure) before the onset of the experiment, and had only been cut once or twice a year, since at least the year 2000.

2.2. Experimental design

In each meadow (n = 11), six circular plots with a diameter of 20 m were established, with at least 5 m buffer zone between the plots (11 meadows × 6 plots = 66 plots; for details on the experimental design see Fig. 1 in Andrey et al., 2016). Six different management treatments were randomly assigned to the six plots and were applied consistently for five years. The treatments were control, irrigation only (medium intensity), fertilization only (medium intensity), and a combination of both irrigation and fertilization at three different intensity levels (low, medium, high). This setup thus comprised a land-use intensity treatment and a partial-crossed factorial design of fertilization and irrigation at medium intensity. In the combined irrigation and fertilization treatments, amounts applied were 1/3 (low intensity), 2/3 (medium intensity) or 3/3 (high intensity) of the quantity theoretically needed to achieve maximum hay yield under local conditions and a mowing regime consisting of two hay harvests per year (according to Sinaj et al., 2009). In each year, sprinkler irrigation was applied weekly from mid-May to beginning of September with 10, 20 or 30 mm of water applied, depending on the intensity level of the irrigation treatment, and corresponding to the standard-farm irrigation amount proposed for the particular geographic region (according to Calame et al., 1992). The plots were not irrigated when >20 mm rain had fallen during the previous week. In spring and after the first hay harvest of each year, the fertilized plots received a water-dissolved solution of organic dried manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium-sulphate (K₂SO₄), corresponding to the standard-farm liquid manure (i.e. slurry: 2.4 kg N, 2 kg P₂O₅, and 8 kg K₂O per m³ of solution; according to Sinaj et al., 2009). The total fertilizer amount added (kg N ha⁻¹ year⁻¹) depended on the theoretical local hay production potential, calculated from pre-experimental hay yield and site elevation (for details see Appendix A in Andrey et al., 2016).

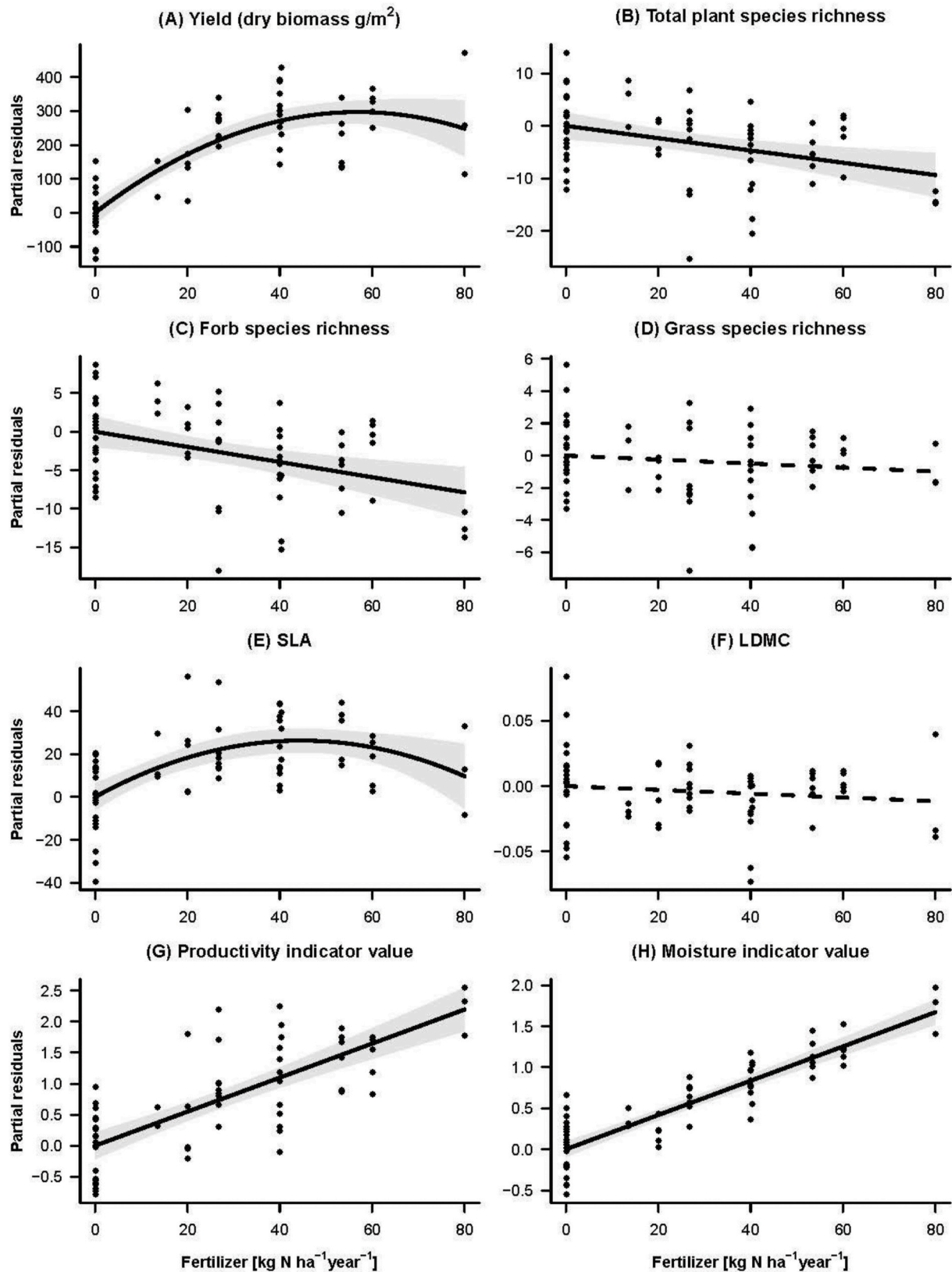


Fig. 1. The effect of total fertilizer amount (continuous fixed effect) on A) yield, B) total plant species richness, C) forb species richness, D) grass species richness, E) community-weighted mean of specific leaf area (SLA), F) community-weighted mean of leaf dry matter content (LDMC), G) mean productivity indicator value, and H) mean moisture indicator value. Shown are the partial residuals (after subtracting the effect of irrigation) and predictions with 95% confidence intervals from the linear mixed-effect models. When significant, the quadratic relationship is shown (see also Table 1). Each dot represents one experimental plot ($n = 66$), the continuous lines indicate significant, the dashed lines non-significant relationships.

2.3. Vegetation and biomass data

In July 2015, we recorded the vegetation of all plots before the first mowing, in a 2 m × 4 m subplot within each treatment plot. We identified all vascular plants and estimated the percentage cover per species. Yield (i.e. dry biomass production) of each treatment plot was quantified twice by clipping the vegetation, once before each hay harvest, at a height of 6 cm in two 1.6 m² rectangles adjacent to the vegetation sampling plot (for details on the arrangement of plots within a site see Fig. 1 in Andrey et al., 2016). Then, the two samples were pooled, dried at 105 °C for 72 h and weighed to quantify the yield per square meter.

2.4. Community-weighted mean traits and mean ecological indicator values

We requested trait data of all sampled vascular plant species from the TRY – Plant Trait Database (Kattge et al., 2011) to compute community-weighted mean traits of specific leaf area (SLA; leaf area per leaf dry mass [mm²/mg]) and leaf dry matter content (LDMC; leaf dry mass per leaf fresh mass [g/g]) for each treatment plot. As woody species only occur as seedlings in mown grasslands and therefore play no significant role in this land-use type, but might differ strongly in their traits, we excluded woody species (6 out of 211) from the calculations. SLA was available for 181 (88.3%) and LDMC for 166 (81.0%) of the 205 remaining herbaceous species. We computed the median value per trait based on all records and used the cover-weighted community mean of each trait per plot for further analysis. Moreover, based on the available ecological indicator values of all sampled vascular plant species, we calculated cover-weighted mean indicator values for soil nutrient contents and moisture (values ranging from 1 to 9; see Ellenberg et al., 2001) of each plot. We use the term “indicator value for productivity” because the nutrient indicator value was proposed to be only weakly related to soil nutrient content and rather reflects site productivity (i.e. plant biomass; Schaffers and Sykora, 2000).

2.5. Statistical analysis

All statistical tests were performed using R version 3.5.1 (R Core Team, 2018). We used linear mixed-effect models (lmerTest package; Kuznetsova et al., 2017) fitting meadow, i.e. study site (11 levels) as random factor to correct for elevational and further site-specific differences. As the amount of fertilizer applied depended on the pre-experimental hay yield and site elevation, the amount of fertilizer per treatment varied among the eleven sites. We therefore included fertilization (total amount of N kg ha⁻¹ year⁻¹, which is proportional to the amount of P and K applied) and irrigation (total amount of water) as continuous fixed effects instead of fitting the experimental treatments as categorical fixed factor. We tested for fertilization and irrigation effects on the species richness of all vascular plants and on forb (including legumes) and grass (i.e. graminoids including *Poaceae*, *Cyperaceae* and *Juncaceae*) species richness separately, as well as on yield, community-weighted mean traits, and mean ecological indicator values. As fertilization and irrigation are partially correlated in the design (plots receive lowest and highest fertilization and irrigation levels together), we lack the power to test for the interaction between them. We further calculated the cumulative cover of vascular plants and of forbs and grasses separately, as well as the grass-forb-cover ratio to test whether the treatments caused shifts in plant functional group abundances. In order to test for non-linear effects of fertilization and irrigation, we fitted models with quadratic terms for these factors in addition to the linear terms. Given the correlation between fertilization and irrigation, we could not fit quadratic terms for both in the same model. We therefore fitted models with quadratic terms for either fertilization or irrigation and if both quadratic effects were significant, we compared models with AIC to determine which term described the data best. The quadratic term for irrigation was only significant in one model (SLA) but the model

with a quadratic term for fertilization had a lower AICc (580.45 vs. 583.58). We therefore do not discuss quadratic irrigation effects further. To test whether the different amounts of nitrogen applied along the elevational gradient had different effects, we fitted an interaction between elevation and fertilization. As the interaction of elevation with fertilization or irrigation did not significantly affect vascular plant species richness, we excluded it from the final analysis and do not discuss it further. For all models, we calculated R^2 as the marginal coefficient (proportion of variance explained by fixed factors alone) and the conditional coefficient (proportion of variance explained by both, fixed factors and random factor) of determination for mixed-effect models (Nakagawa and Schielzeth, 2013; MuMin package: Barton, 2018, Table 1).

In order to detect species-specific responses to fertilization and irrigation, we carried out model-based community analyses (mvabund package; Wang et al., 2020). The function *manyglm* fits a generalized linear model to a matrix of species abundances (percentage cover), by fitting univariate models to each taxon and then summing the test statistics to get the overall community response (Warton et al., 2012). We conducted this analysis with species occurring in at least seven study sites (28 out of 211 species; see Fig. A1). The model included fertilizer (linear and quadratic terms) and irrigation amount, as well as meadow as fixed effects, and used a negative binomial error distribution.

3. Results

3.1. Effects of fertilization and irrigation on yield and vascular plant species richness

We found a quadratic relationship between yield and fertilization, showing an average maximum yield already at 58 kg N ha⁻¹ year⁻¹ and no increase in yield at higher fertilizer values. The species richness of all vascular plants and forbs decreased, on average, by 6 and 5 species, respectively, per 50 kg N of added fertilizer (ha⁻¹ year⁻¹), grass species richness was not affected (Table 1; Fig. 1). Interestingly, irrigation had no effect on yield and species richness. We further found a quadratic relationship between the total cover of vascular plants and fertilization, and no effects of fertilization and irrigation on the cover of forbs and grasses or on the grass-forb-cover ratio (Table 1).

3.2. Effects of fertilization and irrigation on community composition, community-weighted mean traits and mean ecological indicator values

In our plots, the cover of nitrophilous grasses such as *Arrhenatherum elatius*, *Dactylis glomerata*, *Helictotrichon pubescens* and *Trisetum flavescens*, and nitrophilous forbs such as *Heracleum sphondylium*, *Lathyrus pratensis* and *Taraxacum officinale* aggr. increased with high fertilization or irrigation levels. Simultaneously, the cover of initially abundant species, which prefer nutrient poor soil conditions, such as *Briza media* and *Bromus erectus* significantly decreased with increasing fertilization and *Onobrychis vicifolia* significantly decreased with increasing irrigation levels (Fig. A1).

Moreover, we found a hump-shaped relationship between SLA and fertilization, with maximum SLA at intermediate fertilization. While the mean indicator values for productivity and moisture increased with greater amounts of fertilizer applied, LDMC was not affected (Table 1, Fig. 1). Irrigation had no effect on community-weighted mean traits and mean ecological indicator values (Table 1).

4. Discussion

Semi-natural grasslands are frequently fertilized and are irrigated in dry regions to increase their productivity. This land-use intensification is causing strong declines in grassland biodiversity in the lowlands and is leading to a large-scale homogenization of grassland communities and loss of their functional diversity. Here, we show that fertilization in

Table 1

Summary of linear mixed-effect models with meadow fitted as random factor, testing the effects fertilizer ($\text{kg N ha}^{-1} \text{ year}^{-1}$; including quadratic term when significant) and irrigation (mm of water added per m^2) on yield (dry biomass production in g/m^2), total plant species richness, forb species richness, grass species richness, community-weighted mean of the specific leaf area (SLA) and leaf dry matter content (LDMC), cover-weighted mean indicator values for soil productivity and moisture (based on Ellenberg indicator values), cumulative plant cover and separately for forb and grass cover as well as the grass-forb-cover ratio. R^2 is given as marginal coefficient (proportion of variance explained by the fixed factors alone) and conditional coefficient (proportion of variance explained by both, the fixed factors and the random factor) of determination for mixed-effect models. Significant differences are indicated by bold p-values ($P < 0.05$).

	Yield		Total plant species richness		Forb species richness		Grass species richness	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Intercept	342.42	<0.001	50.27	<0.001	39.7	<0.001	10.48	<0.001
Fertilizer	10.44	<0.001	-0.12	0.009	-0.1	0.006	-0.01	0.354
Fertilizer ²	-0.09	<0.001	-	-	-	-	-	-
Irrigation	1.69	0.156	-0.09	0.338	-0.07	0.329	-0.02	0.427
R^2_m	0.56		0.14		0.13		0.04	
R^2_c	0.73		0.33		0.45		0.07	

	SLA		LDMC		Mean productivity indicator value		Mean moisture indicator value	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Intercept	206.03	<0.001	0.24	<0.001	4.35	<0.001	4.24	<0.001
Fertilizer	1.18	<0.001	< -0.01	0.381	0.02	<0.001	0.01	<0.001
Fertilizer ²	-0.01	0.001	-	-	-	-	-	-
Irrigation	0.02	0.908	< -0.01	0.496	0.01	0.384	< -0.01	0.598
R^2_m	0.23		0.03		0.17		0.18	
R^2_c	0.50		0.26		0.65		0.81	

	Cumulative plant cover		Forb cover		Grass cover		Grass-forb-cover ratio	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Intercept	116.95	<0.001	59.39	<0.001	64.93	<0.001	53.66	<0.001
Fertilizer	1.15	0.002	0.19	0.259	0.13	0.365	-0.06	0.525
Fertilizer ²	-0.02	0.010	-	-	-	-	-	-
Irrigation	0.39	0.206	0.04	0.917	0.06	0.844	0.05	0.824
R^2_m	0.12		0.02		0.02		0.01	
R^2_c	0.42		0.36		0.11		0.29	

particular, decreases vascular plant species richness in mountain hay meadows. Fertilization also changes the composition of the plant community by favoring fast-growing, resource-acquisitive plants (increased mean specific leaf area) and species with increased mean indicator values for productivity and moisture. However, we found that maximum yield can be achieved with a lower addition of fertilizer than the recommended maximum. In contrast, we did not find an effect of irrigation alone on species richness or functional composition. This suggests that keeping fertilizer inputs as low as possible is critical for maintaining high plant diversity in mountain grasslands, provided that the land-use and disturbance regime is retained.

4.1. Treatment effects on yield and vascular plant richness

We found that fertilization strongly reduced vascular plant species richness. This corroborates previous results obtained from grasslands (Rajaniemi, 2002; Kleijn et al., 2009; Müller et al., 2016a), including Swiss mountain grasslands (Lessard-Therrien et al., 2017). Fertilization likely reduced grassland diversity because it led to increased light competition and the shading out of smaller species by taller plants (Hautier et al., 2009). While an increase in yield with fertilization is well established (Humbert et al., 2016), we find that there is no further increase beyond $58 \text{ kg N ha}^{-1} \text{ year}^{-1}$. This suggests that farmers might reduce their costs by applying less fertilizer, without compromising on yield. At the same time, they could reduce environmental pollution and by reducing fertilization from 80 to $50 \text{ kg N ha}^{-1} \text{ year}^{-1}$ they could increase plant species richness by about 3.5 species (referring to our $2 \text{ m} \times 4 \text{ m}$ plots; Fig. 1). The saturating response of yield to fertilization might be explained by competitive exclusion of small subordinate species by tall species as light competition becomes more intense (Grime, 1998; Werger et al., 2002). This is supported by the hump-shaped response of cumulative plant cover to fertilization, indicating a loss of vegetation

layers at high fertilization. Moreover, the loss of species richness at high fertilization might reduce biomass production (Grace et al., 2016; Jochum et al., 2020), and a reduction of plant species richness following fertilization has been shown to lower productivity over time (Isbell et al., 2013).

In the present study, we found no effect of irrigation on yield. This was surprising, and in contrast to DeMalach et al. (2017), as increasing yield is the reason why farmers irrigate grasslands. In addition, we found no evidence that irrigation impacts plant species richness, revealing that the negative effect on the overall plant and forb species numbers reported for high intensity managed plots in Lessard-Therrien et al. (2017; same experiment but data collected in 2014 and fitted the experimental treatments as a categorical fixed factors) were probably mostly due to fertilization, while the immediate positive effect (after one year, i.e. in 2011) reported in Andrey et al. (2014) was not visible anymore after five years. In their global meta-analysis, DeMalach et al. (2017) also found non-significant effects of water addition on plant species richness. Interestingly, in their study from semiarid annual grasslands in the US, Eskelinen and Harrison (2015) found that irrigation effects can be context dependent: on nutrient poor soils, irrigation alone had only little impact but a combined irrigation and fertilizer treatment caused a species turnover, decreased diversity and increased productivity, while on nutrient-rich soils, irrigation alone increased productivity and additional fertilization had no further effect. This may suggest that irrigation alone did not increase yield, due to nutrient limitation in our experimental sites.

4.2. Treatment effects on functional composition and functional response traits

Despite the overall decline and the reduced forb species richness, the species richness of grasses was not affected by increasing fertilization.

This is in line with Socher et al. (2013) who studied the effects of different land-use types on vascular plant species richness in German grasslands. In fertilized plots, they found fewer vascular plant species overall but a higher proportion of grass species compared to unfertilized ones. They argued that tall grass species replaced smaller ones and outcompeted smaller forb species. Lessard-Therrien et al. (2017) found a negative effect of high combined fertilization and irrigation levels on forb and grass species richness, which indicates that the negative effects, which was not detected again for grasses in this study, might not be linear across all study sites, but may have some tipping points. In contrast to Rudmann-Maurer et al. (2008), who reported higher legume and lower graminoid cover in fertilized plots, we found no treatment effects on the cover of functional groups. One explanation might be that nutrient-loving species replaced other species, while cover values of the functional groups remained similarly: in our plots, fertilization simultaneously increased the cover of nitrophilous species and decreased the cover of species preferring poor conditions. This indicates that broad functional groups, i.e. grasses and forbs, are too crude to capture land-use effects because other characteristics of species are important in determining their response to environmental factors.

In contrast, functional response traits might be better suited to reflect land-use effects on the functional composition of grasslands: For example, Pfestorf et al. (2013) found SLA being the most sensitive functional trait to predict responses to increasing land-use intensities and fertilization, and Busch et al. (2019) found tall-growing species with high SLA being associated with high land-use intensity and fertilization, both in German grasslands. However, in our study SLA had a hump-shaped response to fertilization, with highest values at intermediate fertilizer levels. This seems counterintuitive, but it might be because of the increasing abundances of nitrophilous species with intermediate SLA values: *Dactylis glomerata*, *Trisetum flavescens* and *Taraxacum officinale* aggr.

Unexpectedly, we found no effects of irrigation on community-weighted mean traits. This is in contrast to Müller et al. (2016b) who found irrigation effects on reproduction- and growth form-related plant traits when comparing traditionally irrigated and non-irrigated grasslands. Although they did not analyze irrigation effects on traits related to resource use, one would expect irrigation effects on SLA, as low SLA is linked to drought resistance. Thus, it might be that the duration of our experiment was still too short to detect irrigation effects on functional response traits.

4.3. Treatment effects on mean indicator values

We found that fertilization increased the abundance of plant species with high mean productivity indicator values. This agrees with many other studies on fertilizer effects on plant communities (Blüthgen et al., 2012). Moreover, fertilization also increased the mean indicator values for moisture. This is similar to Boch et al. (2019a) who found higher mean moisture indicator values with increasing site productivity in inner-alpine dry valleys of Switzerland. Dostál et al. (2017) reported a positive relation between productivity and moisture indicator values because species from nutrient-rich habitats also tend to occur in wet places. In our study, the cover-weighted mean indicator values for productivity and moisture were also positively correlated ($R^2 = 0.59$), explaining their increase with fertilization. However, irrigation alone had no direct effect on mean indicator values in the studied grasslands. This again might suggest that the duration of our experiment was too short to detect irrigation effects on the functional composition of the investigated grasslands.

5. Conclusions

We showed that diversity and functional composition of mesic mountain grasslands are highly sensitive to fertilization, but are relatively resistant to irrigation. The negative effects were apparent after

four years (Lessard-Therrien et al., 2017) and it is plausible that they will become stronger with time (Humbert et al., 2016).

Although it has been suggested that irrigation is required for maintaining farming activities in dry mountain regions such as the Valais (Riedener et al., 2014), we found no effect of irrigation on yield in the investigated mesic hay meadows. However, while mesic mountain hay meadows seem to be less affected, sprinkler irrigation has devastating effects on the biodiversity of xeric grasslands, such as the inner-alpine steppes, because of strong compositional changes and the loss of rare and threatened specialist plant and animal species (Volkart, 2008).

Our finding that maximum yield can be achieved at intermediate fertilizer levels is important from an applied, agronomical and conservation point of view. It suggests that farming costs, environmental pollution and biodiversity loss can all be reduced without compromising yield. Altogether, our findings highlight the need to maintain non-intensive grassland management regimes and keep fertilizer inputs as low as possible to conserve the high biodiversity of mountain grasslands.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2020.111629>.

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