The effect of *Rhinanthus alectorolophus* on productivity in Swiss meadows

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Preface

The presented bachelor's thesis is part of a larger project from the "Marktplatz für Forschungsfragen Naturschutz" led by the "Forum Biodiversität Schweiz der Akademien der Naturwissenschaften (SCNAT)" and the "Konferenz der Beauftragten Natur und Landschaft (KBNL)". This platform aims at enhancing the connection and exchange between practice and research in conservation biology. For this purpose, questions from conservation practitioners are collected and mediated to research with the aim of developing evidence-based solutions for practical problems. The results will be published on the website of the "Marktplatz für Forschunsgfragen Naturschutz" (www.kbnl.ch).

This bachelor thesis was conducted in close collaboration with Nico Heer and Fabian Klimmek who also studied a *Rhinanthus*-related topic at the Institute of Plant Sciences (IPS), University of Bern, in the context of their bachelor thesis. Data collection, preparation and analyses were performed together but the topics of the three theses differed. Fabian Klimmek studied "The effect of *Rhinanthus alectorolophus* on plant biodiversity in Swiss meadows" (Klimmek 2015) and Nico Heer "The effect of *Rhinanthus alectorolophus* on community composition and structure in Swiss meadows" (Heer 2015). Accordingly I will cite my colleagues when referring to their results.

Abstract

Hemiparasites are known to influence community structure and ecosystem functioning, but the underlying mechanisms are not fully understood. For hemiparasites, host plants are the source of water and nutrients below-ground, but competitors for light above-ground at the same time. Hemiparasites can reduce host biomass, and in this way considerably affect competitive networks of plant communities. When parasitic pressure in grassland is high enough, the reduced host biomass should result in substantial changes in plant diversity. To investigate this productivity-diversity relationship, 427 vegetation relevés in 47 meadows in three distinct regions of Switzerland were conducted along a density gradient of *Rhinanthus alectorolophus.*

We showed that a *Rhinanthus* density of around 30% reduced productivity by about a quarter. As expected this decline in productivity maximized plant diversity. Further, we showed that with relative *Rhinanthus* densities above 40%, the hemiparasite biomass compensated the productivity loss due to parasitism. The results demonstrate for the first time that these changes within a plant community can be explained by the presence of *Rhinanthus.* In summary, the results highlight that hemiparasites have profound effects on grasslands. Because plant diversity increases and productivity is only partially reduced, these results indicate that *Rhinanthus* can be considered as an effective tool in restoring plant diversity in grasslands.

Introduction

Semi-natural grasslands are characterized by the ability to host a high diversity of species of different trophic levels. Compared to other vegetation types of similar size, grasslands in central Europe are among the plant communities with highest species densities worldwide (Wilson et al. 2012). Nowadays, semi-natural grasslands are threatened from two sides. On the one hand, the intensification of agricultural production, particularly increased nutrient inputs, promote few highly competitive species and thereby decrease overall species diversity (Allan et al. 2014). On the other hand, the abandonment of unproductive or inaccessible areas has led to the loss of these habitats in the last few decades (Poschlod et al. 2009). These two trends have occurred throughout Central Europe and the Nature Conservancy Council (NCC) has therefore recognised grasslands as internationally threatened habitats (NCC 1989). To reverse these negative trends, immense efforts have been made with the aim to restore and maintain highly valuable grasslands. That this is not an easy task is supported by the fact that the restoration of grasslands is a long-term process, which can last more than ten years (Pywell et al. 2004). One of the main obstacles in grassland restoration is that high meadow productivity, resulting in the dominance of competitive plant species, often grasses, prevents the establishment of target species (Walker et al. 2004). Methods to restore high productive grasslands are difficult and the expected results are not always obtained, mostly because the high amounts of nutrients in the soil are difficult to remove. Drastic measures like the removal of nutrient-rich topsoil are effective but also very costly (Mudrák 2014).

As an alternative approach for accelerating the restoration of grasslands, the introduction of native hemiparasitic plants has been proposed (Davis et al. 1997, Smith et al. 2003, Mudrák and Lepš 2010). The impact of hemiparasites are to a certain degree host specific (Joshi 2000, Press and Phoenix 2005) and, in many cases, the dominant species in a community are affected most. Further, hemiparasites are often short-lived and after the dieback, relatively early in the year, gaps are created in the vegetation, which can be colonized by other plants (Joshi et al. 2000). The newly established species can then profit from the leaf litter of hemiparasites, which have a higher concentration of nutrients than their hosts. Because this litter decomposes fast, the released nutrients in the topsoil are available for other species (Spasojevic and Suding 2011, Fisher et al. 2013). As a result, the presence of hemiparasites is expected to positively affect the diversity of grasslands (Davies et al. 1997, Pywell et al. 2004, Bullock and Pywell 2005, Westbury et al. 2006).

Because hemiparasitc plants have such profound effects on plant communities, they can be considered either as keystone species or ecosystem engineers. As keystone species, because of their ability to facilitate coexistence and diversity through parasitizing selectively or density-dependent competitive species (Pennings and Callaway 1996, Smith 2000). Hemiparasites can also alter the abiotic environment, mostly soil humidity and the availability of nutrients. They can therefore also be considered ecosystem engineers (Press and Phoenix 2005).

Rhinanthus alectorolophus (European yellowrattle; from now on referred as *Rhinanthus*) is an annual root hemiparasite of the Orobanchaceae family that commonly occurs in extensively managed grasslands in Central Europe (Joshi et al. 2000). *Rhinanthus* is a facultative hemiparasite, which means that it can complete its life cycle and produce seeds without a host. If attached to a host, growth and seed production are greatly increased (Matthies and Egli 1999). *Rhinanthus* attempts to develop vascular continuity with the roots of its potential hosts through the penetrating structure of the haustorium (Riopel and Timko 1995). Field observations suggest that *Rhinanthus* parasitizes a wide range of host species (Weber 1976). Experiments have further shown that *Rhinanthus* can use many different species and even individuals of its own species simultaneously as hosts (Matthies 1995, Prati et al. 1997, Joshi et al. 2000). The impact of *Rhinanthus* on various host species varies. Grasses generally show the greatest reduction in biomass while the biomass of forbs is less reduced and legumes show variable responses (Ameloot et al. 2005).

Rhinanthus has the ability to reduce the productivity of the plant community in which it occurs due to their low nutrient and water-use efficiency (Phoenix an Press 2005) and the damage inflicted to their hosts (Cameron et al. 2008). However the effects on productivity are controversially discussed. While Ameloot et al. (2005) or Fisher et al. (2013) showed that *Rhinanthus* decreased productivity in grassland by 26%, other studies found the contrary effect (Joshi et al. 2000, Spasojevic and Suding 2011). Long-term studies also concluded that a productivity loss due to *Rhinanthus* disappears with time (Ameloot et al. 2006a, Westbury et al. 2006). These different results could be explained by the fact that the effect of *Rhinanthus* on host species depends on several factors. One factor is the number of *Rhinanthus* individuals per m^2. Ameloot et al. (2006b) experimentally showed that above-ground biomass significantly decreases with the number of *Rhinanthus* plants per plot. Cameron et al. (2005) demonstrated that nutrient concentration in the soil could also be a factor that is crucial to how much host productivity is reduced by *Rhinanthus*. Further factors are the distance to the host plant (Keith et al. 2004), the age of the host at infection, because young plants suffer more than older ones, and the number of consecutive years of infection (Seel and Press 1996).

Simultaneously with the productivity decrease, the diversity of the host community often increases (Pywell et al. 2004, Westbury et al. 2006, Klimmek 2015). Although there is much evidence to indicate that *Rhinanthus* has an effect on plant diversity in grasslands, the mechanism for this is not yet completely understood. It seems that grassland diversity can be enhanced by the presence of *Rhinanthus* when host species are dominant. When the preferred host species are competitive dominant species, their suppression by *Rhinanthus* allows the expansion of subdominant species and therefore community diversity increases (Davies et al. 1997). In contrast, if *Rhinanthus* shows preference to penetrate subdominant species, then the diversity of a community tends to decrease (Gibson and Watkinson 1992).

Rhinanthus have several characteristics that make it an effective tool in grassland restoration. As a natural part of many grassland communities, its introduction is desirable for biodiversity. The introduction of *Rhinanthus* is a relatively cheap method. Its seeds are easy to collect and *Rhinanthus* can even be introduced into productive grasslands without experiencing any serious difficulties (Mudrák et al. 2014). Further, *Rhinanthus* does not build a persistent seed bank and the population depends on the seeds produced annually. The population is therefore easy to control. Even when its density increases, early mowing can decrease its density rapidly (Magda et al. 2004).

That the impacts of *Rhinanthus* on grasslands nowadays are still controversial could be due to fact that previous studies compared productivity and diversity of meadows with and without *Rhinanthus*. Such a methodical approach cannot, for example, answer the question whether meadows in which *Rhinanthus* occur are low–productive due to the effect of the hemiparasite on the hosts or whether a low-productive meadow is a prerequisite for *Rhinanthus* to occur (Ameloot et al. 2005). Methodically better and more meaningful would be to investigate the effects of *Rhinanthus* along a density gradient within a meadow. Such an approach allows the comparison of meadows with different environmental conditions (different location, different nutrient contents in the soil).

This new approach was therefore used to investigate the effect of *Rhinanthus* on the productivity of meadows along a density gradient. We hypothesized that the presence of *Rhinanthus* affects the productivity of meadows: (1) *Rhinanthus* reduces the productivity of a grassland. Thus, we expected a decrease of productivity with an increasing *Rhinanthus* density. (2) *Rhinanthus* suppress grasses more than herbs because they are the preferred host species. Subsequently, the effects on aboveground biomass are discussed with respect to plant diversity in grasslands and in relation to the potential use of *Rhinanthus* as a practical tool for the diversification of semi-natural grasslands.

Materials and methods

Study system

The study was carried out in three regions in Switzerland. To cover an altitudinal gradient, we conducted the vegetation surveys in the surroundings of Bern, in the Bernese Oberland, and in the Canton of Valais. The altitude ranged from 504 m a.s.l. (Bern) up to 1946 m a.s.l. (Schynige Platte, Bernese Oberland). The maximum geographic distance between the regions was about 80 km. Around Bern we investigated 30 meadows, in the Bernese Oberland 13 and in the Valais 4 meadows.

Vegetation sampling

The vegetation surveys were conducted from mid-May to the end of June 2015. The vegetation surveys were thus at the peak of the growing season of *Rhinanthus* (May for meadows around Bern and June for meadows at higher altitudes). In each meadow we sampled all plant species along a density gradient of *Rhinanthus*. To achieve this, we distributed nine 20×20cm plots in each meadow. Three plots were placed randomly in patches with a relatively high *Rhinanthus* density, three in medium density patches and three in patches with a low density of *Rhinanthus*. In each plot, we identified all plant species and estimated their percentage cover. The percentage cover per plant species was estimated by eye and defined as the proportion of the ground occupied by a perpendicular projection of the aerial parts of individuals of each species. The total plant cover per quadrat was recorded as the sum of the cover of individual species, which, due to the over-layering of different species, can have a value greater than 100%. Where species identification was difficult, we used species aggregates and species names "sensu lato" (s.l.) rather than identifying them to taxonomically lower levels. To harvest the total above-ground biomass, the vegetation was cut approximately 20mm above ground level using secateurs. Samples were then sorted into three categories: *Rhnianthus*, grasses, and herbs. Biomass samples were dried in an oven at 80°C for at least 48 hours and weighted.

Statistical analysis

To test our hypotheses we applied linear mixed-effect models using the *nlme* package (Pinheiro et al 2015) in R 3.2.2 (R Development Core Team 2015). To illustrate the effect of an increasing *Rhinanthus* density on meadow productivity, we constructed a linear mixed-effect model with the relative *Rhinanthus* biomass per plot as a linear and, when significant, as a quadratic term. Regions and observers were included as covariates. Meadows were included as a random term to account for the differences among the meadows. We applied the model to the total biomass of a plot and to the biomass excluding *Rhinanthus* (from now on referred as host biomass).

To show the effect of an increasing *Rhinanthus* density on diversity and community composition we used the package *vegan* (Oksanen et al. 2015) to calculate the Shannon index and Pielou's evenness, see Heer (2015) and Klimmek (2015).

Results

The effect of *Rhinanthus* on the productivity of meadows

We found a significant curved-linear relationship between the total biomass (biomass including *Rhinanthus*) and the relative *Rhinanthus* biomass (Figure 1a, Table 1). The favourable *Rhinanthus* density with the highest species richness of the plant community was 31% relative *Rhinanthus* biomass (Klimmek 2015). At this density level, the productivity of the meadow was on average reduced by 26%. Furthermore, we found a significant host biomass decrease (p = 0.0002; R^2 = 0.55) with an increasing relative *Rhinanthus* biomass (Figure 1b; Table 1).

Table 1. Anova results for the total biomass, host biomass (total biomass-biomass *Rhinanthus*), biomass of herbs and of grasses. We conducted the following linear mixed-effect model (lme) for all four measures: Y ~ Region*(*Rhinanthus* density + I (*Rhinanthus* density ^2) + observer, random =~I meadow. In each case, we computed models with *Rhinanthus* density as a quadratic and as a linear parameter and selected the best model according to *p*-values.

Biomass		Inlcuding *Rhinathus*		Excluding *Rhinanthus*		Herbs		Grasses	
	df	*F*-value	*p*-value	*F*-value	*p*-value	*F*-value	*p*-value	*F*-value	*p*-value
(Intercept)	1	503.0947	**<.0001**	538.9743	**<.0001**	319.5635	**<.0001**	148.0884	**<.0001**
Region	2	1.4349	0.2491	3.8952	**0.0277**	7.6872	**0.0014**	0.61949	0.5428
rel. *Rhinanthus* biomass linear	1	6.2622	**0.0128**	195.4796	**<.0001**	63.8523	**<.0001**	64.07011	**<.0001**
rel. *Rhinanthus* biomass quadratic	1	12.3491	**0.0005**	14.0102	**0.0002**	4.2477	**0.04**	-	-
Observer	2	12.2734	**<.0001**	10.3786	**<.0001**	0.385	0.6807	10.20821	<.0001
Region x rel. *Rhinanthus* biomass linear	2	0.4416	0.6434	0.7091	0.4928	2.831	0.0602	1.68767	**0.1864**
Region x rel. *Rhinanthus* biomass quadratic	2	0.137	0.8721	0.1663	0.8469	1.4251	0.2418	-	-
			R^2: 0.46		R^2: 0.55		R^2: 0.35		R^2: 0.42

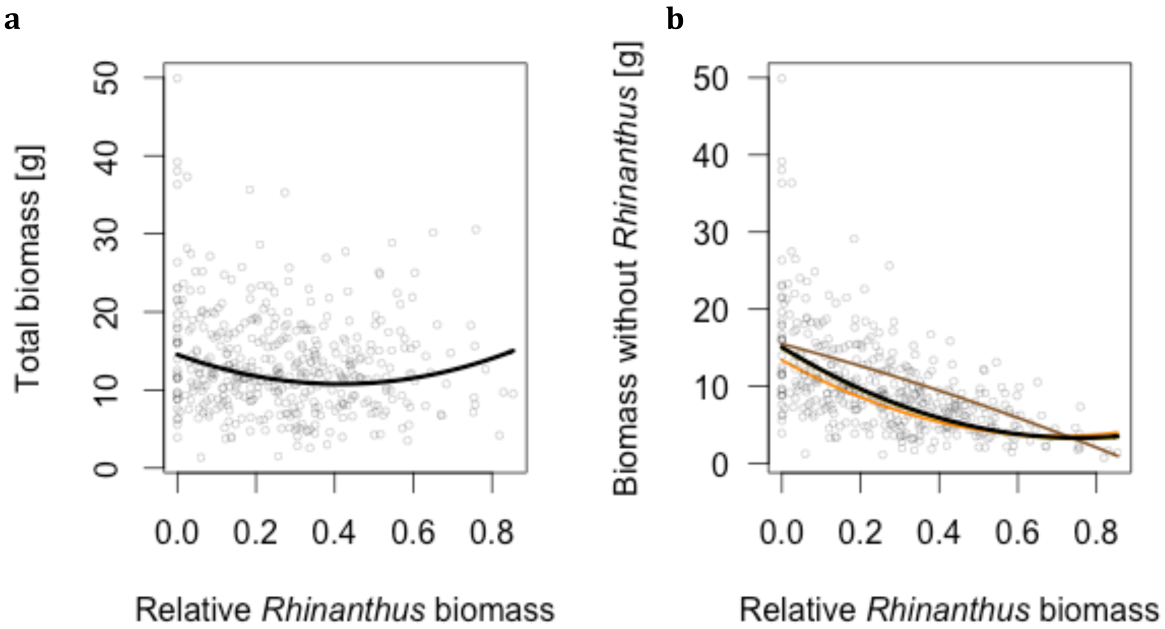

Figure 1. Relationships between a) total biomass and b) biomass without *Rhinanthus* and the relative *Rhinanthus* biomass. The black line represents the regression of the whole model. Coloured lines indicate differences among the three study regions Bern (yellow), Bernese Oberland (orange), Valais (brown). The regions were only shown when they were significantly different from each other.

<u>The effect of *Rhinanthus* on the productivity of herbs and grasses</u>

For the biomass of herbs we observed an u-shaped pattern with an increasing relative *Rhinanthus* biomass (Figure 2a), whereas the biomass of grasses decreased linearly (Figure 2b).

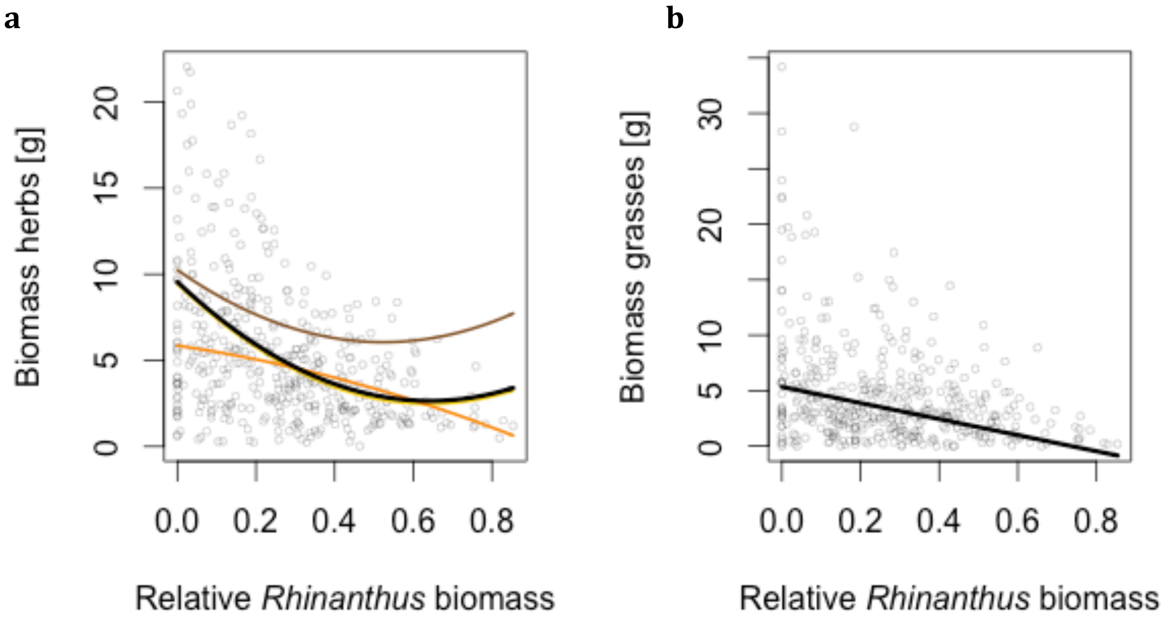

Figure 2. Relationships of the biomass of herbs and the biomass of grasses with the relative *Rhinanthus* biomass. The black line represents the regression of the whole model. Coloured lines indicate differences among the three study regions Bern (yellow), Bernese Oberland (orange), Valais (brown). In both cases the quadratic and linear relationship were tested. The linear relationship was included when the quadratic relationship was not significant.

Discussion

We examined the relative *Rhinanthus* biomass as a factor which affects the productivity of grasslands and found an u-shaped relationship. The highest decrease of biomass was recorded when the relative *Rhinanthus* biomass in a meadow reached 40%. Due to the new approach for investigating community structure along a *Rhinanthus* density gradient, the productivity reduction can be explained by the effect of the parasite on the hosts. Furthermore, we showed that the productivity of grasses decreased linearly, whereas the productivity of herbs showed an u-curved relationship along the *Rhinanthus* density gradient.

The presence of hemiparasitic plants can have a profound impact on their hosts. After successful parasite attachment, host plants exhibit reduction in biomass accumulation. This impact of *Rhinanthus* along a density gradient in grasslands is visible in figure 1b. With increasing *Rhinanthus* density the hemiparasite most likely extracts more water and nutrients by its hosts. This leads to a continuous productivity decrease of meadows if biomass is weighed without the biomass of *Rhinanthus*.

However, the picture changes when considering the total biomass, e.g. including the *Rhinanthus* biomass. It seems that *Rhinanthus* incorporated the absorbed nutrients into its own biomass (Figure 1a), and nutrients might remain in the system. This would indicate that the soils of the meadows probably do not become nutrient-poorer. In this context figure 1a implies that the presence of *Rhinanthus*, up to a density of 60%, does not fully compensate the reduction in host biomass due to parasitism. In this range the presence of *Rhinanthus* leads to a slight overall reduction in productivity up to 26% by a relative *Rhinanthus* density of 35%. This value is confirmed by other studies. In a quantitative literature review, Ameloot et al. (2005) found that the total above-ground biomass of the vegetation was on average reduced by 26% in experimental sowing studies; or Fisher et al. (2013) showed that parasitism by *Rhinanthus* caused an overall decrease in total community biomass of 25.8%. Klimmek (2015) showed that at a *Rhinanthus* density of 31%, the diversity of grasslands is maximised (+ 12% species richness). For hemiparasites this means that they are surrounded by many species and plants of different functional groups. Press and Phoenix (2005) reviewed that parasitic plants simultaneously parasitize and compete with its neighbouring plants at the same time. Their own productivity is therefore dependent on the quality of the hosts and the strength of competition from neighbouring plants. In a diverse meadow *Rhinanthus* parasitizes not only high quality hosts, like legumes and grasses, and therefore its own biomass is not maximal and cannot compensate the loss of biomass due to parasitism. When *Rhinanthus* density in a meadow is higher than 60%, the hemiparasite seems to compensate the biomass loss (Figure 1a). It can be argued that such high and productive densities of *Rhinanthus* are only possible if the environmental conditions and the management regime of the meadow are optimal for *Rhinanthus*. Optimal environmental conditions include that good quality hosts surround *Rhinanthus* and therefore *Rhinanthus* can maximise its own productivity. Seel and Press (1993) showed that the growth of hemiparasites is not only a function of attachment, as has been previously reported by Klaren and Janssen (1978), but also a function of the host type. In the case of *Rhinanthus*, it could be shown that the hemiparasite is most successful in terms of growth, biomass accumulation and reproduction when growing in association with N-fixing legumes (Seel and Press 1993; Westbury 2004; Cameron et al 2006). According to this, host quality is reported to decrease from N-fixing legumes over grasses to non-leguminous forbs (Gibson and Watkinson 1991, Cameron et al 2006). The fact that *Rhinanthus* is short-lived and can reach high densities in grasslands makes *Rhinanthus* very unpopular with farmers since grasslands where *Rhinanthus* occur always seem to be low productive (Magda et al 2004, Ameloot et al. 2006). But the short annual life cycle and absence of a persistent seed bank makes *Rhinanthus* dependent on annual seed production. Therefore, the abundance of *Rhinanthus* in grasslands can easily be managed with an appropriate mowing regime. Especially by an annual species without a persistent seed bank, an interruption in the renewal of adult plants through the mortality of juveniles has an immediate effect on population density. An early mowing, which will affect a maximum number of juveniles, can enable the eradication of very dense *Rhinanthus* population within 2 to 3 years (Magda et al. 2004). The appropriate timing of the first mowing to harm *Rhinanthus* population is in fact 2-3 weeks earlier than Swiss farmers are allowed to, when they participate in subsidized agricultural programms to promote biodiversity (BLW 2013). Therefore, farmers must apply for permission to regulate high *Rhinanthus* densities with an appropriate mowing regime.

According to the literature, we assumed that grasses are preferred hosts of *Rhinanthus* and that the prevalence of *Rhinanthus* for grasses should increase the productivity of herbs in grasslands. With our results we could not support this assumption. When the effect on productivity of herbs (fig. 2a) and grasses (fig. 2b) is considered separately, it becomes apparent that the productivity of grasses decreased linearly, whereas the biomass of herbs showed an u-shaped relationship. The increase at the right end of the herbs productivity curve is probably due to the bias that such high densities of *Rhinanthus* (>60%) can only be reached in very productive meadows and therefore productivity again increases. The result that productivity of grasses is not more pronounced compared to the productivity of herbs is a bit surprising. The assumption that host preference of *Rhinanthus* is associated with a decline in the proportion of grasses and simultaneously increases the proportion of forbs was shown in several studies (Davies et al. 1997; Cameron et al 2005). Press and Phoenix (2005) mentioned that *Rhinanthus* preferred grasses because they have an abundant and fine root systems close to the surface. This makes it easy for *Rhinanthus* to locate and penetrate. Besides that grasses are the most common components of the communities in which *Rhinanthus* occurs (Gibson and Watkinson 1989), which makes them particularly susceptible to parasitic infection. In contrast, forbs remain undamaged due to their ability to express defence responses against the invading haustorium of the parasite (Cameron et al. 2006; Rümer et al. 2007).

A reason why we found no differences between the productivity of grasses compared to the productivity of herbs are probably due to the fact that we distinguished only between the functional groups of grasses and herbs. That means that within the biomass of herbs the one of legumes is included. The productivity decline of herbs might therefore be explained by the productivity decline of legumes. If we would have separated the biomass of herbs and legumes, we may have been able to see a productivity decline for legumes and in addition a slight increase in the productivity of herbs. The fact that productivity of grasses and herbs similarly decreased along the *Rhinanthus* density gradient implies that *Rhinanthus* is a generalist and shows no host preference. Therefore, *Rhinanthus* tends to parasitize the most abundant species of the community in which it occurs. Only when the evenness of a meadow is high it can be assumed that *Rhinanthus* on average parasitizes more high quality hosts (Davies et al. 1997). The presence of *Rhinanthus* therefore favours a higher degree of equity in grasslands which otherwise would be dominated by only a few high competitive species (Klimmek 2015).

All discussed results indicate that *Rhinanthus* has profound effects on grasslands. The removal of water and nutrients reduces the photosynthetic rate, biomass and competitive ability of their hosts (Jiang et al. 2003; Pywell et al. 2004; Press and Phoenix 2005; Cameron et al. 2008). These effects decrease the above-ground biomass of the infected community. Reduction on productivity can have far-reaching consequences for a plant community. Reduced above-ground biomass leads to lower above-ground competition. Further, in contrast to most grassland species, *Rhinanthus* is short-lived and can reach high densities. As a consequence, gaps in the vegetation are left after the dieback of *Rhinanthus*. These gaps can facilitate the establishment of new species, as demonstrated in experimental grassland plots with *Rhinanthus* (Joshi et al. 2000; Pywell et al. 2004; Ameloot et al. 2005; Westbury et al. 2006). With our study we supported the findings of previous studies. As mentioned above, the slight biomass decrease of 26% correlates with the highest plant species diversity in semi-natural grasslands (Klimmek 2015). Furthermore, Heer (2015) showed that plant height and relative *Rhinanthus* biomass correlate in a negative linear relationship. This shift in community mean height indicates that *Rhinanthus* promotes smaller species in plant communities.

In summary, our results highlight that intermediate *Rhinanthus* densities between 30-40% indeed result in a decrease in productivity. Because the decrease in productivity is accompanied by the suppression of dominant competitive species, *Rhinanthus* supports the diversity and therefore the stability of plant communities (Bullock and Pywell 2005; Ameloot et al 2008; Klimmek 2015). *Rhinanthus* therefore seems to be a useful tool in the restoration of semi-natural grasslands.

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Erklärung

Gemäss Art. 28 Abs. 2 RSL 05

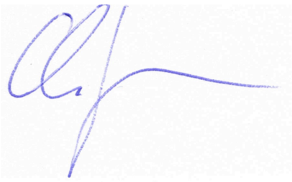
Name/Vorname: Zwahlen Christoph
Matrikelnummer: 10-918-803
Studiengang: Biologie

Bachelor Titel der Arbeit: The effect of Rhinanthus alectorolophus on productivity in Swiss meadows

Leiter der Arbeit: S. Boch und D. Prati

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe r des Gesetztes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist. Ich gewähre hiermit Einsicht in diese Arbeit.

Ort/Datum: Bern 14.02.206
Unterschrift:



Ch. Zwahlen