Perspectives in Plant Ecology, Evolution and Systematics 32 (2018) 22–29

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Hemiparasite-density effects on grassland plant diversity, composition and biomass

Nico Heer[a], Fabian Klimmek[a], Christoph Zwahlen[a], Markus Fischer[a,b], Norbert Hölzel[c], Valentin H. Klaus[c,e], Till Kleinebecker[c], Daniel Prati[a], Steffen Boch[a,b,d,*]

[a] Institute of Plant Sciences, University of Bern, 3013 Bern, Switzerland
[b] Botanical Garden, University of Bern, 3013 Bern, Switzerland
[c] Institute of Landscape Ecology, University of Münster, 48149 Münster, Germany
[d] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland
[e] ETH Zürich, Institute of Agricultural Sciences, 8092 Zürich, Switzerland

ARTICLE INFO

Keywords:
Biomass quality
Community mean traits
Near infrared spectroscopy
Rhinanthus alectorolophus
Yield

ABSTRACT

Hemiparasitic plants are considered ecosystem engineers because they can modify the interactions between hosts and other organisms. Thereby, they may affect vegetation structure, community dynamics and facilitate coexistence as they are able to reduce interspecific competition by parasitizing selectively on competitive species and promote subordinate ones. In agri-environmental schemes, introducing the hemiparasite *Rhinanthus* has therefore been suggested as a low-cost method to increase grassland plant diversity, which is still subject to debate.

The majority of previous studies simply compared sites with and without hemiparasites. However, as hemiparasite effects are most likely density-dependent, we present a novel approach assessing the effect of *Rhinanthus alectorolophus* density on grassland plant diversity, yield and community biomass quality. Moreover, we investigated whether functional plant composition and community mean traits are affected by *Rhinanthus* density, which has been largely neglected in previous studies.

The relationship between species richness and relative *Rhinanthus* biomass followed an optimum curve with highest values at 31% relative *Rhinanthus* biomass. At this *Rhinanthus*-biomass level, species richness was increased by 12% and yield decreased by 26% compared with plots without *Rhinanthus*. At relative *Rhinanthus* biomass > 60%, species richness was even lower than in plots without *Rhinanthus*. Overall, the biomass of grasses and the cumulative cover of legumes decreased linearly with increasing relative *Rhinanthus* biomass. Community mean trait analysis revealed that an increasing *Rhinanthus* density shifts the community composition towards smaller plant species. Biomass quality was not affected by increasing relative *Rhinanthus* biomass.

In summary, our results of increased plant diversity – in line with a slightly lower yield but similar community biomass quality – indicate that *Rhinanthus* is a suitable biological tool for grassland restoration.

1. Introduction

In Central Europe, land-use intensification has led to homogenous grassland communities with only few highly competitive species and a loss of the overall diversity and ecosystem functions (Wesche et al., 2012; Allan et al., 2014; Soliveres et al., 2016; Gossner et al., 2016). To reverse this trend, low intensity farming is currently promoted by agri-environmental schemes (e.g. Kleijn et al., 2009) to restore diverse and highly valuable grassland ecosystems. However, high residual soil fertility is a key factor limiting restoration success (Pywell et al., 2007, Klaus et al., 2011). Various attempts to overcome this problem have been suggested: Nutrient removal by frequent mowing or grazing tends to be slow and, particularly in the case of phosphorus, ineffective (Bullock and Pywell, 2005), whereas the more straightforward removal of top-soil is effective but costly (Hölzel and Otte 2003, Mudrák et al., 2014). An alternative and cost-effective tool for grassland restoration counteracting the inhibitive effects of dominant species is the introduction of native parasitic plants into these ecosystems (Davies et al., 1997; Smith et al., 2003; Mudrák et al., 2014).

The genus *Rhinanthus*, a member of the large parasitic Orobanchaceae family, is the most common root hemiparasitic genus throughout temperate Europe (Ameloot et al., 2005). Hemiparasites are

* Corresponding author at: Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland.
E-mail address: steffen.boch@wsl.ch (S. Boch).

https://doi.org/10.1016/j.ppees.2018.01.004
Received 21 November 2016; Received in revised form 31 October 2017; Accepted 30 January 2018
Available online 19 February 2018
1433-8319/

photosynthetically active and consume water and nutrients from their hosts (Watson, 2009; Westwood et al., 2010), but also a considerable amount of assimilates and secondary compounds may be taken up (Adler, 2000; Těšitel et al., 2010). *Rhinanthus* spp. are generalists, parasitizing many different species (Gibson and Watkinson, 1991). Their roots form haustoria on any root they encounter (Cameron and Seel 2007). *Rhinanthus* is therefore more often successfully parasitizing hosts with a diffuse and wide spreading root system, such as grasses, than the ones with e.g. taproot during their whole lifecycle (Mudrák et al., 2016). Moreover, forbs with high nutrient contents, e.g. legumes, or forbs without adequate defence mechanisms preventing penetration and access to the xylem have been suggested to be better-suitable hosts (Seel and Press, 1993; Matthies, 1996; Ameloot et al., 2005; Cameron et al., 2006; Matthies, 2017). *Rhinanthus*plants are able to reduce interspecific competition by parasitizing competitive species or by exerting density-dependent control of dominant plants, thereby facilitating coexistence and promoting the stability of natural communities (Phoenix and Press, 2005; Těšitel et al., 2015a). Moreover, it has been suggested that in particular annual hemiparasites can create gaps after senescence, which in turn promotes the establishment of other species (Joshi et al., 2000; Bullock and Pywell, 2005; but see also Davies et al., 1997). *Rhinanthus* spp. have been recommended as tool for grassland restoration as they are a natural part of European grasslands. In addition, because they are annuals, their density can be controlled easily by mowing before seed ripening (Magda et al., 2004; Bullock and Pywell, 2005; Westbury et al., 2006; Mudrák et al., 2014). Today, *Rhinanthus* spp. are already part of seed mixtures for biodiversity promoting areas (BPA) in Switzerland. However, whether effects on plant diversity are positive (e.g. Bardgett et al., 2006; Fibich et al., 2016) or negative (Gibson and Watkinson, 1992) is still unclear (see also Ameloot et al., 2005 for a meta-analysis).

Similarly, while most studies found *Rhinanthus* to reduce community biomass (Ameloot et al., 2005, 2006), some experimental studies found a biomass increase (Joshi et al., 2000). The intuitive expectation of many farmers is a reduction of yield by the presence of hemiparasites, which makes *Rhinanthus* very unpopular for them (Magda et al., 2004; Ameloot et al., 2006). Related to this, it is often presumed that *Rhinanthus* reduces the nutritional value of the yield with severe losses in fodder quality. Such fodder quality decreases might be driven by changes in the functional plant composition of infested grasslands and should then be reflected by changes in nitrogen, mineral and fibre contents in plant biomass. However, as this has not been tested systematically, it remains dubious whether hemiparasites indeed affect biomass quality.

Moreover, the functional role of hemiparasites in grasslands is still unclear (see Quested et al., 2003). As they are known for their low nutrient and water-use efficiency (Phoenix and Press, 2005) it can be assumed that they may affect the abiotic environment, which might be reflected by changes in mean environmental indicator values of the vegetation, e.g. for moisture and nutrient availability (e.g. Landolt et al., 2010). In addition, whether hemiparasites affect plant community structure and composition, indicated by changes in functional groups and community mean traits, was also largely neglected in previous studies (but see Demey et al., 2015; Mudrák et al., 2016). In particular, hemiparasites may lead to changes in resource-related community mean traits such as specific leaf area and leaf dry matter content as well as competition-related ones such as mean plant height, or dispersal- and colonization-related ones such as seed mass.

So far, studies investigating hemiparasite effects on grasslands used an ‘all or nothing’ approach, comparing sites with and without hemiparasites (e.g. Gibson and Watkinson, 1992; Joshi et al., 2000; Stein et al., 2009; Mudrák and Lepš, 2010). However, this approach may not be fully informative as it does not take the variation in *Rhinanthus* density into account, although hemiparasite effects are most likely density-dependent. Thus, it is unclear whether there is a *Rhinanthus*-density–grassland plant diversity optimum. In addition, different sites may not be fully comparable as they might differ in other environmental conditions apart from the presence of the hemiparasite. It has been shown that the abiotic site conditions such as water and nutrient availability have profound interactive effects on hemiparasite and host biomass and fitness (Těšitel et al., 2015b). Thus, in studies showing decreases in productivity in the presence of *Rhinanthus* (e.g. Davies et al., 1997) it remains unclear whether *Rhinanthus* drives this decrease or simply prefers low-productive conditions (Ameloot et al., 2005; Bullock and Pywell, 2005).

Here, we present results from an alternative approach testing whether varying *Rhinanthus alectorolophus* densities affect the plant diversity, plant community composition, productivity and biomass quality along *Rhinanthus*-density gradients within sites. Studying density effects within a site instead of between sites ensures similar environmental conditions among the replicates. Furthermore, to more explicitly explain plant community patterns and test for individual species responses along the *Rhinanthus* gradient, we used hierarchical Huisman-Olff-Fresco (HOF) models, a novel approach for modelling species response curves.

We therefore conducted a multi-site study, investigating 47 sites in three distinct regions in Switzerland allowing us to draw more general conclusions than investigating only a single region. This may further allow us to formulate recommendations on the suitability of *Rhinanthus* in grassland restoration. In particular, we tested whether and how increasing *Rhinanthus alectorolophus* density affects 1) plant diversity, 2) species composition reflected by community mean functional traits and environmental indicator values, and 3) grassland productivity and biomass quality.

2. Methods

2.1. Study system

To enhance representativeness and generality of results and conclusions, we conducted our study in 47 meadows in three distinct regions in Switzerland: the Bernese lowland ($N = 30$), the Bernese Oberland ($N = 13$) and the Valais ($N = 4$). Sites were selected by accurate point coordinates on the occurrence of *Rhinanthus alectorolophus* provided by Info Flora (www.infoflora.ch), the national data and information center of the Swiss flora, as well as by own observations. All sites were non-intensively managed meadows which could be assigned to communities of the Arrhenatherion alliance in the Bernese lowland and mainly to communities of the Polygono-Trisetion alliance in the two regions at higher altitudes (sensu Delarze et al., 2015). We considered a site to be suitable if it was well accessible, not mown when the vegetation was assessed and when *Rhinanthus alectorolophus* was present in varying densities. In addition, the site had to be visually homogeneous, e.g. that it could be assigned to one vegetation type. Altitude ranged from 504 m.a.s.l. (Bernese lowland) to 1946 m.a.s.l. (Schynige Platte, Bernese Oberland). The maximum geographic distance between the regions was approximately 80 km. Mean annual precipitation varies among the regions with around 700 mm in the Valais, 1000 mm in the Bernese lowland and 2000 mm in the Bernese Oberland.

2.2. Vegetation and biomass data

Between mid-May and beginning of June 2015, we sampled the meadows in the Bernese lowland, in mid-June the ones in Valais and between mid and end of June the ones in the Bernese Oberland, to account for the different developmental stages of the vegetation along the altitudinal gradient. Within each meadow, we placed nine 20 cm × 20 cm plots along a density gradient of *Rhinanthus alectorolophus* (named *Rhinanthus* hereafter). For this, we first visually subdivided each grassland in zones with low, medium and high *Rhinanthus* density and randomly placed three plots in each zone to maximize the