



Modelling the effect of belowground herbivory on grassland diversity



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ABSTRACT

One challenging question in ecology is to explain species coexistence in highly diverse temperate grassland plant communities. Within this context, a clear understanding of the consequences of belowground herbivory for the composition and the diversity of plant communities continue to elude ecologists. The existing body of empirical evidence reveals partly contradictory responses ranging from negative to neutral or positive effects of belowground herbivory on grassland diversity.

To reveal possible mechanistic grounds for these discrepancies, we extended an existing simulation model of grassland communities based on plant functional types to include root herbivory. This enabled us to test the effects of different feeding modes that represent different herbivore guilds. For each belowground feeding mode, we systematically varied the intensity and frequency of herbivory events for three different levels of soil fertility both in the presence and absence of additional aboveground grazing.

Our modelling approach successfully reproduced various empirically reported diversity responses, merely on the basis of the different feeding modes. Different levels of plant resource availability affected the strength, but not the direction of the belowground herbivory effects. The only exception was the scenario with low resource levels, which promoted neutral (neither positive nor negative) diversity responses for some of the feeding modes. Interestingly, aboveground biomass production was largely unaffected by diversity changes induced by belowground herbivory except in the case of selective feeding modes that were related to specific functional traits.

Our findings provide possible explanations for the broad spectrum of belowground herbivory effects on plant community diversity. Furthermore, the presented theoretical modelling approach provides a suitable conceptual framework to better understand the complex linkage between plant community and belowground herbivory dynamics.

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1. Introduction

Root herbivores play an important, but often underappreciated role in grassland ecosystems. It is known that soil-borne pests can reduce yield by up to 15% (Clements et al., 1990), but the effect of root herbivory on individual plant fitness, and thus on the outcome of competition, may vary widely between different herbivorous groups and under different environmental conditions (Zvereva and Kozlov, 2012). For example, a moderate infestation with micro-herbivores such as nematodes may result in compensatory growth or even overcompensation (Bardgett et al., 1999a,b), whereas the effects of macro-herbivores such as insect larvae are more likely to

be detrimental and may even result in the plant's death (Seastedt and Murray, 2008). Moreover, some authors state that generalist root herbivores such as *Agriotes* spp. larvae are likely to feed mostly on those plant species whose roots are most abundant in the habitat of the larvae (Sonnemann et al., 2012), while others have shown that insect root herbivores have feeding preferences or even specialize on individual plant species, because palatability of root tissues varies widely between species (Van Dam, 2009). As the potential for migration is generally limited in soil dwelling insects, host specificity might be strongly connected to the oviposition behaviour of adults (Johnson et al., 2006). Thus, it is expected that the specificity or generality of root herbivores have important consequences for plant competition and species coexistence (Stevens and Jones, 2006; Schallhart et al., 2012).

The role of insect root herbivores in shaping plant community structure, succession and diversity has long been studied (for review articles see for example: Brown and Gange, 1990; Mortimer et al., 1999; Hunter, 2001; Blossey and Hunt-Joshi, 2003), but various field- and greenhouse experiments yielded different, often

Abbreviations: PFT, plant functional type; ZOI, zone of influence.

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contradictory results. For example, [Brown and Gange \(1992\)](#) found, via insecticide application, that root feeding insects accelerate secondary succession, which in that case reduced plant diversity. In contrast, under experimental conditions [De Deyn et al. \(2003\)](#) showed that invertebrate root herbivores feed selectively on roots of dominant species (higher root quality and accessibility) therefore enhancing diversity (see also [Van Ruijven et al., 2005](#)). However, other authors suggested that individual effects of different soil organisms may cancel each other out ([Blomqvist et al., 2000](#); [Bradford et al., 2002](#); [Wurst et al., 2008](#)).

In general, root herbivory is extremely difficult to study under field conditions, since the actual process of root feeding cannot be observed. Greenhouse experiments carry the disadvantage that due to logistical constraints root herbivore and plant communities are reduced to few or single taxa. Moreover, there is evidence that additional factors such as nutrient availability, the management regime and successional stage might greatly influence root herbivore distribution ([Parker and Seeley, 1997](#); [Czárán, 1998](#); [Lefko et al., 1998](#); [Callahan et al., 2003](#)) and its effect on plant community structure and diversity ([Mortimer et al., 1999](#); [Schadler et al., 2004](#); [Coupe et al., 2009](#)). Therefore, we believe that, alongside further empirical work, mechanistic modelling can provide a suitable tool for improving our theoretical understanding of root herbivore effects on plant communities.

To the best of our knowledge, belowground biotic interactions of plants with other taxa have been rarely considered in ecological theory and models. Previous food web models at the scale of plant communities already included belowground herbivory, but these models have been designed to study carbon and nitrogen fluxes in agricultural ecosystems, grasslands and forests rather than to investigate soil food web effects on plant species diversity (see for examples: [de Ruiter et al., 1998](#); [Schroter et al., 2003](#)). There are useful conceptual frameworks to study the effects of above-belowground interactions on individual plant growth ([Masters et al., 1993](#); [Schroter et al., 2004](#)), which have already been successfully applied in a modelling approach ([Meyer et al., 2009](#)). However we are not aware of theoretical work that focused on root herbivore effects on whole plant communities. In this context, individual based modelling may help to identify how individual plant responses to herbivory scale up to community dynamics, which may reveal key processes that are responsible for the contrasting results found in empirical studies.

In this study, we apply an individual-based modelling approach to study the response of grassland communities constituted of plant functional types ([May et al., 2009](#)) to different preference modes and intensities of belowground herbivory. We thereby distinguish between five modes of belowground herbivory representing the behaviour of the most important, naturally occurring root herbivorous groups and taxa (i.e. generalist and specialist micro-, meso-, and macro-herbivores). Furthermore, we investigated the interactive effects of preference modes with the strength and the frequency of herbivory events. To account for environmental factors, we considered the interplay of belowground herbivory, resource availability and aboveground biomass removal (i.e. grazing by domestic livestock).

Our hypotheses are: (1) Belowground herbivory can have a negative, neutral or positive impact on plant diversity depending on environmental conditions and/or the mode of herbivory, and (2) belowground herbivory has a positive impact on plant diversity only if plant types with aboveground dominance are preferentially fed on.

2. Methods

To test our hypotheses we extended the model IBC-grass (Individual Based Community model of grassland), which is an

established, mechanistic simulation model that simulates grassland communities, initialized with 81 plant functional types (PFTs), in a spatially explicit approach ([May et al., 2009](#)). Competition is modelled using the zone-of-influence (ZOI) approach ([Schwinning and Weiner, 1998](#); [Weiner et al., 2001](#); [Berger et al., 2008](#)). More specifically, the model considers size-asymmetric above-ground competition for light and size-symmetric belowground competition for water and nutrients ([May et al., 2009](#)).

The original model was designed to evaluate the functional response of plant communities towards aboveground grazing under different local environmental conditions. The new modifications address the community response towards belowground herbivory considering different modes of herbivore foraging strategies.

The full description of the original model and our modifications are given in the supplement following the ODD protocol (overview, design concepts, details) for describing individual-based models ([Grimm et al., 2006, 2010](#)). Here, we only give a brief overview of the model including the new modules for belowground herbivory.

2.1. Overview of the IBC-grass model

The vegetation, composed of plant individuals of different PFTs, grows on a square grid of 128 by 128 discrete grid cells, each representing 1 cm² in size. Plant individuals are centred in one of the grid cells but can cover several cells depending on their size. Each individual plant is assigned to one of 81 PFTs, spanning a four-dimensional space of the trait syndromes consisting of: (1) 'growth form', (2) 'maximum plant size', which is correlated with seed mass and dispersal distance, (3) 'resource utilization', correlating with stress tolerance, and (4) 'response to grazing' correlating with specific leaf area. All trait syndromes are parameterized with specific trait attribute parameters that vary within three levels (3⁴=81 PFTs, [May et al., 2009](#)).

The biomass of each plant individual is made up of three compartments; shoot-, root- and reproductive biomass (i.e. seeds). Individual plants compete for resources in two distinct layers (one aboveground, i.e. light, and one belowground) using a zone-of-influence (ZOI) approach (e.g. [Berger and Hildenbrandt, 2000](#); [Schwinning and Weiner, 1998](#)). These ZOIs are represented by circular areas around the plant's central position. In both layers, ZOI sizes are defined by the biomass of the respective plant compartment (i.e. shoot or root). Whenever ZOIs overlap, the individuals compete within this overlapping area. Aboveground competition is assumed to be partially asymmetric (i.e. the larger plant takes up more resources in the overlapping area proportionally to its mass and shoot geometry, see Eq. (A3b) in supplement), while belowground competition is assumed to be size symmetric (i.e. resources are shared equally; resource uptake is, however, regulated by PFT-specific maximum resource utilization rates).

The processes of resource competition, plant growth and plant mortality as well as disturbances are considered in each time step during the vegetation period. Seed production, seed dispersal and seedling establishment are limited to certain weeks of the year (Table A2 in supplement). Winter dieback of above-ground biomass and mortality of seeds are considered at the end of the vegetation period.

The single cells contain resources, which are taken up by the local plant or are shared among the locally competing plants (i.e. overlapping ZOIs). The resources a cell can provide are kept constant in space and time.

Plant growth depends on the limited resource uptake of the two ZOIs (i.e. above- or belowground). When a limitation occurs, the plant growth allocation is affected; in the aboveground zone (i.e. light is limiting) shoot growth is proportionally favoured, while belowground limitation leads to enhanced root growth ([Snyder and](#)

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