Shoot herbivory by grasshoppers has stronger effects on root morphology than clipping

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Abstract Studies investigating the effect of aboveground herbivory on plants often use clipping to simulate the effects of herbivores, for practical reasons. However, herbivore movements and transfer of oral secretions during herbivory may cause a different response in plant physiology and morphology compared to clipping. While studies have compared effects of real herbivory vs. clipping on biomass production, plant physiology, and shoot morphology, no study has compared such effects on root morphology. Therefore, we investigated the effect of herbivory by grasshoppers, herbivory simulated by clipping, and no herbivory on root morphological traits of ten grassland plant species. Root morphological traits were differently affected by the two herbivory treatments. Grasshopper herbivory significantly changed root morphology toward thinner roots with increased specific root length and root area, and decreased root tissue density compared to untreated control plants. Clipping had mostly similar, but weaker effects on root morphology than grasshopper herbivory. On the species level, grasshopper herbivory led to strongest changes in root morphology in almost all cases. In contrast, depending on the species, clipping resulted in varying root morphological trait values similar to grasshopper-damaged plants, or in some cases, more closely aligned with control plants. Though clipping was partly able to mimic the effects of herbivory by grasshoppers, results also indicate that, depending on the species, grasshopper herbivory had different but mostly stronger effects. We, therefore, recommend that future studies apply herbivory with real herbivores to better reflect natural responses in plants.

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and related processes that root morphological traits mediate.

**Keywords** Root morphology · Root traits · Clipping · Herbivory · Grasshopper

### Introduction

Aboveground herbivory is omnipresent and can have diverse effects on plants (Crawley 1989; Maron and Crone 2006). Besides direct effects on aboveground biomass (Maron 1998; Hawkes and Sullivan 2001) herbivory by vertebrates and invertebrates can cause indirect effects via changes in plant physiology (Karban and Myers 1989; Howe and Jander 2008) with consequences for biomass allocation (Briske and Richards 1995; Johnson et al. 2016), and the morphologies of shoots (Milewski et al. 1991; War et al. 2012) and roots (Heinze 2020). Studies on herbivory often use artificial herbivory, such as clipping, rather than real herbivores (Lehtilä and Boalt 2004), because artificial herbivory has logistical advantages (Hjältén 2004). In contrast to real herbivory, clipping removes plant biomass without herbivore-induced effects, like transfer of oral secretions (e.g., saliva; Bergman 2002; van Kleunen et al. 2004), chewing vibrations by herbivores (Appel and Cocroft 2014), or bending motions in shoots due to herbivore weight (Kothari and Burnett 2017), that are suggested to be important for physiological responses in plants. Nevertheless, clipping was shown to induce changes in plant physiology (Vergés et al. 2008; Hernán et al. 2019), and the morphologies of shoots (Dostálek et al. 2016; Reese et al. 2016) and roots (Thorne and Frank 2009).

However, comparative studies of clipping and real herbivory revealed differences in plant responses in many cases (see Lehtilä and Boalt 2004; Fuchs et al. 2017; Liu et al. 2018). These previous comparative studies focused on the effects of clipping and real herbivory on biomass production, plant physiology, secondary compounds and aboveground morphology, but not on root morphology. Therefore, we specifically asked: Do clipping and real herbivory differ in their effect on root morphology?

### Methods

#### Study site and species

The study was performed at an experimental field site of the University of Potsdam (N52°24’29.76”, E13°1’13.74”, Brandenburg, Germany) to provide more natural growth conditions for plants than greenhouses (see e.g., Heinze et al. 2016; Forero et al. 2019). To test effects of different herbivory application methods on root morphological traits and whether these effects differ among plant functional groups, we selected ten common grassland species, five grasses, and five forbs. All ten species were used in a previous experiment on insect herbivory and root morphology in the meadow near the experimental field site (Heinze 2020; Heinze et al. 2020). The five grasses were *Arrhenatherum elatius* (L.) J. Presl and C. Presl., *Dactylis glomerata* L., *Holcus lanatus* L., *Luzula campestris* L. and *Poa pratensis* L. and the five forbs were *Achillea millefolium* L., *Plantago lanceolata* L., *Rumex acetosella* L., *Taraxacum officinale* Kirschner et al. and *Trifolium pratense* L.. Seeds of all species were collected by hand in the meadow in summer 2019.

#### Experimental preparation and set-up

Seeds of all species were germinated on washed sand (grain size: 2 mm; Brun & Böhmi; Potsdam, Germany) in sterile plastic chambers (32 cm × 50 cm × 14 cm; Meyer, Rellingen, Germany) in a greenhouse (min/max temperature 15 °C/25 °C; relative humidity 33%/90%; additional light: 140 μmol * s⁻¹ * m⁻²; 12/12 h light/dark) in May 2020. Pots (Deepots D25L: volume 0.41 l; height 25 cm; diameter 5 cm; Stuewe & Sons, Tangent, Oregon, USA) were filled with a soil:sand mixture consisting of a 1:1 mixture of sieved (mesh size: 5 mm) native soil collected from the field site and washed sand. This soil:sand mixture facilitated washing roots afterward. In early June 2020, two-week-old, similar-sized seedlings were planted in the prepared pots, with one seedling per pot. After planting, young seedlings were allowed to acclimatize for one week. Seedlings that died during this time were replaced. In mid-June 2020, the planted pots were brought to the experimental site. To protect experimental plants from herbivory by slugs and insects, all pots were placed in an experimental
cage (1.6 × 3.6 × 1.5 m) that was placed on black foil (PPX woven fabric, Meyer; Germany) and completely covered with fly mesh (mesh size: 0.7 mm; Meyer; Germany), including the bottom. Within the experimental cage, pots were placed in trays. Each tray contained one replicate of each herbivory application method per species. Within each tray pots were randomly arranged. Each species × herbivory treatment (see below) was replicated 5 times resulting in 150 pots [10 species × 3 herbivory treatments × 5 replicates (i.e., trays)]. Plants were grown for four weeks prior to the herbivory treatment. During this time plants were watered two times per week with tap water. We rotated the trays, which held the pots, within the cage bi-weekly, to reduce potential differences in abiotic conditions within the experimental cage.

**Herbivory treatment**

The herbivory treatment was imposed in July 2020. It consisted of (1) no herbivory (control), (2) clipping, and (3) herbivory by grasshoppers. We used common grasshoppers (*Chorthippus parallelus*) because they are generalist herbivores (Branson and Sword 2009) and the main herbivores in the meadow at the field site (see Heinze 2020; Heinze et al. 2020). Prior to the grasshopper herbivory treatment, individuals of *C. parallelus* were caught in the meadow. Grasshoppers were kept in a cage (60 × 90 × 30 cm; completely covered with fly mesh) and starved for one day before usage in the experiment. We used the herbivore-inclusion method with nylon bags (mesh size 0.3 mm; 22 × 30 cm; Saketos; Deutschland) to apply herbivory by grasshoppers (see e.g., Bezemer et al. 2013; Heinen et al. 2018). To do so, each pot was enclosed for two days with a nylon bag containing one grasshopper. After two days of grasshopper exposure nylon bags were removed and the biomass removal (i.e., damage) by grasshoppers was measured according to Heinze (2020). All plants showed shoot damage between one and ten percent (see Online Resource Table S1). Immediately after the grasshopper treatment, the clipping treatment was performed on the tray level. We clipped a comparable amount of leaf biomass per species as removed in the respective grasshopper treatment pots, to prevent differences in biomass removal. The plants of the no herbivory treatment were left unclipped.

To prevent differences in abiotic conditions between the different herbivory treatments, pots of the clipping and control (i.e., no herbivory) treatment were covered with nylon bags for the same time as the grasshopper treatment pots. Furthermore, to avoid confounding effects of herbivory-induced volatiles, whose effective radius can range from 60 to 100 cm (Heil 2014), we grouped the pots of the three treatments and spaced these three groups at least two meters apart for the duration of the herbivory treatment application. After the application of the different herbivory treatments, plants were grown for another two weeks. During this time, plants were watered and pot-holding trays were shifted as described above.

**Measurements**

After seven weeks, shoots were harvested and roots were carefully washed. To investigate whether different herbivory treatments influenced root morphological traits of plants, a subsample of five randomly chosen secondary roots (i.e., first order branch from taproot (see Freschet et al. 2021); maximum diameter: 0.48 mm) of the whole root system of each plant was analyzed using the WinRhizo scanner-based system (Regents Instruments, Inc., Canada) to determine root diameter and length. Roots were then dried (48 h, 80 °C) and weighed to obtain root mass of the subsample. Specific root morphological traits (except average diameter, AD) were calculated according to Ryser and Lambers (1995) and Wright and Westoby (1999): specific root length (SRL; cm mg⁻¹), specific root surface area (SRSA; cm² mg⁻¹) and root tissue density (RTD; mg cm⁻³). For the calculation of RTD, the volume of 0.1 mm diameter classes was summed as recommended by Rose (2017). Shoot and root biomass of all experimental plants was dried (48 h, 80 °C) and weighed to assess root:shoot ratio.

**Statistical analyses**

All analyses were performed in R version 3.6.3 (R Development Core Team 2020). Prior to analysis, residuals were checked for homogeneity of variance and tested for normality.

To test whether different herbivory methods affected biomass production and allocation, and root morphological traits across (1) all species and (2) between functional groups, we performed two
separate ANOVAs. To account for the nesting of species within functional groups, we analyzed the data with linear mixed effects models using the “lme4” package (Bates et al. 2015). We used the lmerTest function to estimate P-values and degrees of freedom with type III Kenward–Roger approximation (Kuznetsova et al. 2017).

The model for all species included the predictors ‘species,’ ‘herbivory treatment,’ and their interaction. The model for the functional group included the predictors ‘functional group,’ ‘herbivory treatment,’ and their interaction. Both models tested the effects of the predictors and their interactions on biomass production (shoot, root, total), root:shoot ratio, and morphological root traits (SRL, SRSA, AD and RTD). In the second model, ‘species’ was included as random effect. To test for differences between herbivory treatments in morphological traits across all species, within species, and within functional groups, we performed Tukey HSD tests using the multcomp package (Hothorn et al. 2016).

Results

Herbivory treatment effects on biomass production and allocation

The leaf damage generated by grasshoppers, and thus the amount of tissue removed by clipping as well, was generally low (see Online Resource Table S1). There were no differences in shoot, root, total biomass, nor root:shoot ratio between control, clipped, and grasshopper-damaged plants (Table 1).

Herbivory treatment effects on root morphology

Across all plant species, the different methods of herbivory application affected root morphological traits (P < 0.001 for SRL, SRSA, AD and RTD; Table 1a,b). Herbivory by grasshoppers significantly changed root morphology toward thinner roots with increased SRL and SRSA, and decreased AD and RTD compared to untreated control plants (Fig. 1). Except for SRL, clipping caused the same significant root morphological changes as herbivory, although the response was not as strong (Fig. 1).

Similar patterns in the change of root morphology were observed in both grasses and forbs.

| Table 1 Summary of ANOVA results for biomass production and allocation, and root morphological traits |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Biomass production and allocation | Shoot | Root | Total | Root:Shoot | Morphological root traits | SRL | SRSA | AD | RTD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species (S) | 9 | 120 | 22.5 | 4.43 | < 0.001 | 0.95 | 0.481 | 20.6 | < 0.001 | 17.0 | < 0.001 | 6.73 | 10.4 | < 0.001 | 2.74 | 2.90 | < 0.001 | 0.42 | 0.76 | < 0.001 |
| Herb. Treat. (H) | 2 | 120 | 1.34 | 0.265 | 1.63 | 0.201 | 0.89 | 0.414 | 0.80 | 0.453 | 24.5 | < 0.001 | 15.0 | < 0.001 | 23.8 | < 0.001 | 29.4 | < 0.001 | 20.4 | < 0.001 |
| S x H | 18 | 120 | 0.75 | 0.749 | 1.23 | 0.250 | 0.82 | 0.669 | 0.97 | 0.494 | 1.06 | 0.419 | 1.05 | 0.419 | 1.05 | 0.419 | 1.05 | 0.419 | 1.05 | 0.419 |
| a) | 1 | 8 | 0.01 | 0.981 | 0.04 | 0.840 | 0.01 | 0.959 | 1.24 | 0.298 | 0.68 | 0.433 | 0.02 | 0.8953 | 13.3 | 0.007 | 13.3 | 0.007 | 13.3 | 0.007 |
| b) | 1 | 8 | 0.01 | 0.981 | 0.04 | 0.840 | 0.01 | 0.959 | 1.24 | 0.298 | 0.68 | 0.433 | 0.02 | 0.8953 | 13.3 | 0.007 | 13.3 | 0.007 | 13.3 | 0.007 |
| Func. groups (F) | 1 | 120 | 0.75 | 0.749 | 1.23 | 0.250 | 0.82 | 0.669 | 0.97 | 0.494 | 1.06 | 0.419 | 1.05 | 0.419 | 1.05 | 0.419 | 1.05 | 0.419 | 1.05 | 0.419 |
| F x H | 2 | 136 | 0.26 | 0.744 | 1.44 | 0.242 | 0.56 | 0.574 | 1.06 | 0.349 | 1.02 | 0.306 | 0.08 | 0.928 | 11.1 | 0.001 | 11.1 | 0.001 | 11.1 | 0.001 |

The ANOVAs tested effects for (a) species (ten) and (b) functional group (‘grasses’ vs. ‘forbs’) with herbivory treatment (‘no’ vs. ‘clipping’ vs. ‘grasshopper’) and their interactions on biomass production and allocation (shoot, root, total biomass as well as root:shoot ratio) and root morphological traits (specific root length (SRL), specific root surface area (SRSA), average diameter (AD) and root tissue density (RTD)). Significant effects (P < 0.05) are reported in bold. 

* P < 0.05; ** P < 0.01; *** P < 0.001
(functional group x herbivory treatment interaction: \( P > 0.3 \) for all root morphological traits; Table 1b and Fig. S1). Within both functional groups, individual species showed mainly similar effects in root morphological traits in response to herbivory by grasshoppers vs. clipping (species x herbivory treatment interaction: \( P > 0.1 \) for all root morphological traits; Table 1a), but responses differed in their strength/significance (Fig. 2). In almost all cases, herbivory by grasshoppers led to the highest values for SRL and SRSA and the lowest values for AD and RTD (Fig. 2), especially in species that received lowest biomass loss due to herbivory (see Online Resource Table S1 and Fig. S2). In contrast, roots of the clipped plants showed either similar root morphological trait values as grasshopper-damaged plants or control plants (Fig. 2).

**Discussion**

We observed no impact of herbivory treatment on biomass production and allocation indicating either that plants in this study were able to tolerate (i.e., compensate) minor shoot damage (see e.g., McNaughton 1983; Fornoni 2011), or that the damage level was too low to generate detectable differences in biomass between clipping, grasshopper treatment and untreated plants. However, more importantly, the low level of shoot damage affected root morphological traits of plants in this experiment.

Both methods of herbivory application, mostly increased SRL and SRSA and decreased AD and RTD compared to control plants. Because higher SRL and SRSA presumably increase nutrient uptake efficiency (Thorne and Frank 2009), a change toward thinner roots with increased SRL and SRSA might...
Herbivory treatment:
- No Clipping
- Grasshopper

(a) SRL (cm / mg)
(b) SRSA (cm$^2$ / mg)
(c) AD (mm)
(d) RTD (mg / cm$^2$)

| Species | SRL | SRSA | AD | RTD |
|---------|-----|------|----|-----|
| Ae      | a   | b    | a  | a   |
| Dg      | a   | a    | a  | a   |
| Hi      | a   | a    | a  | a   |
| Lc      | a   | a    | a  | a   |
| Pp      | a   | a    | a  | a   |
| Am      | a   | a    | a  | a   |
| Pl      | a   | a    | a  | a   |
| Ra      | a   | a    | a  | a   |
| To      | a   | a    | a  | a   |
| Tp      | a   | a    | a  | a   |

Grasses
Forbs
be a plant’s response to compensate for herbivory-induced biomass loss (Heinze 2020). Besides removing biomass, damage induces changes in phytohormones concentrations, such as auxin and cytokinins, in plants (Johnson et al. 2016). These phytohormones are involved in shaping root morphology (Lee et al. 2018; Lymperopoulos et al. 2018) and may cause the observed changes in root morphological traits due to clipping and grasshopper herbivory.

Clipping and grasshopper herbivory differ in various ways. For instance, during grasshopper herbivory oral secretions are transferred, which cause physiological responses in plants (Bergman 2002; Howe and Jander 2008). This transfer of oral secretions might induce higher concentrations of phytohormones or different phytohormones such as jasmonic acid (Liu et al. 2011; Xu et al. 2015) which might result in overall stronger effects in root morphology than clipping. Furthermore, grasshopper chewing likely generated vibrations in plant tissue and such motions have been reported to affect physiological responses in plants (Appel and Cocroft 2014). Vibrations might also contribute to the observed differences in root morphology between clipping and herbivory. It is also possible that grasshoppers caused additional root thigmomorphogenesis by bending shoots due to the grasshopper weight during herbivory (see Kothari and Burnett 2017), inducing stretch-activated responses in cell membrane channels, similar to shoot oscillations under wind (Chehab et al. 2009; Telewski 2021).

Although the overall results suggest that clipping had weaker effects on root morphology compared to grasshopper herbivory, a closer look revealed varying treatment responses between species. In about half of the species, herbivory treatments did not impact root morphology significantly, indicating no different effect of clipping and grasshopper herbivory. This is in accordance with findings of comparative studies on artificial and natural herbivory on growth and reproduction (Lehtilä and Boalt 2004). The other species, which interestingly received little or no damage by grasshoppers under natural conditions (see Heinze 2020), showed stronger responses in root morphological traits between the herbivory treatments. Here, grasshopper herbivory led to the strongest changes in root morphology, whereas clipping resulted in root morphological trait values either similar to grasshopper-damaged plants, control plants, or intermediate between the two. These mixed results are in accordance with previous studies suggesting that in some plant species, the different herbivore-induced effects (e.g., transfer of oral secretions) cause stronger physiological and morphological responses than in others (see e.g., Detling et al. 1980; Bergman 2002; Lehtilä and Boalt 2004; Liu et al. 2018).

In this study, we focused on root morphological traits and hence did not measure physiological responses such as changes in phytohormone concentrations. Therefore, we cannot provide specific explanations for the mixed results of clipping versus grasshopper herbivory, especially as species differ in composition of secondary metabolites, which can impact their physiological and morphological response to herbivory (Howe and Jander 2008). Nevertheless, results show grasses and forbs respond similarly to herbivory treatments, suggesting that responses in root morphology to clipping and grasshopper herbivory are more dependent on the plant species than on the plant functional type.

All these effects were observed under artificial conditions in young plants. Although we did not observe pot-bound effects, further studies are needed to verify results in older plants and under natural field conditions. Furthermore, in our experiment there was a slight time difference between grasshopper herbivory and clipping to generate comparable amount of tissue damage in both treatments. We measured root morphology two weeks after the tissue damage, which is known to quickly change phytohormone concentrations and subsequent phenotypical characteristics (Erb et al. 2012). To gain a more comprehensive picture, future studies should test how tissue damage changes a plant’s morphology over time.

As root morphological traits are generally important for occupying soil space, water and nutrient...
uptake processes, decomposition, and interactions with soil biota (Casper and Jackson 1997; Bardgett et al. 2014), any change in root morphology is likely to impact plant-plant competition and feedbacks between plants and soil (Heinz 2020). This implies that different effects on root morphology due to differences between clipping and grasshopper herbivory probably impact plant growth and important ecosystem functions, which root morphological traits mediate. Therefore, our study suggests to apply real herbivory rather than simulated herbivory, especially when the goal is to cover a plant’s full response spectrum and related processes.

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Data availability Data will be made available upon publication.

Code availability Not applicable.

Declarations

Conflict of interest Not applicable.

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