



Herbivory by aboveground insects impacts plant root morphological traits

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Abstract Aboveground herbivory induces physiological responses, like the release of belowground chemical defense and storage of secondary metabolites, as well as physical responses in plants, like increased root biomass production. However, studies on effects of aboveground herbivory on root morphology are scarce and until now no study tested herbivory effects under natural conditions for a large set of plant species. Therefore, in a field experiment on plant–soil interactions, I investigated the effect of aboveground insect herbivory on root morphological traits of 20 grassland plant species. For 9 of the 20 species, all individuals showed shoot damage in the presence of insect herbivores, but no damage in insect herbivore exclusions. In these 9 species root biomass increased

and root morphological traits changed under herbivory towards thinner roots with increased specific root surface. In contrast, the remaining species did not differ in the number of individuals damaged, root biomass nor morphological traits with herbivores present vs. absent. The fact that aboveground herbivory resulted in thinner roots with increased specific root surface area for all species in which the herbivore exclusion manipulation altered shoot damage might indicate that plants increase nutrient uptake in response to herbivory. However, more importantly, results provide empirical evidence that aboveground herbivory impacts root morphological traits of plants. As these traits are important for the occupation of soil space, uptake processes, decomposition and interactions with soil biota, results suggest that herbivory-induced changes in root morphology might be of importance for plant–soil feedbacks and plant–plant competition.

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Introduction

Plants are ubiquitously exposed to aboveground herbivory (Crawley 1989; Maron and Crone 2006).

Aboveground consumption not only affects aboveground biomass (Crawley 1989; Maron 1998) but also induces responses in roots (see e.g., Johnson et al. 2016a). For example, physiological responses to aboveground herbivory include induction of systemic changes and release of secondary metabolites, including defense compounds (e.g., Bardgett et al. 1998; Howe and Jander 2008; Bezemer and van Dam 2005; Karolewski et al. 2010; Johnson et al. 2016a). Physical responses can include increased root biomass production (McNickle and Evans 2018; Sarquis et al. 2019). Increased root biomass production can, however, occur by producing either few thick or multiple thin roots. Furthermore, the fact that aboveground herbivory induces changes in concentrations of phytohormones like auxin and cytokinins (e.g., Johnson et al. 2016a) that besides stimulating overall root biomass production are also involved in the development of lateral roots (Lee et al. 2018; Lymperopoulos et al. 2018) suggests that aboveground herbivory might also influence root morphology.

Although a few studies have tested the effect of aboveground biomass removal on root morphological traits, using clipping (Thorne and Frank 2009), mowing (Leuschner et al. 2013), insecticide application (Pastore and Russell 2012) or short-term application of insect herbivores under artificial conditions (Tiiva et al. 2019) until now no study directly has tested herbivory effects for a large set of species under natural conditions. Therefore, within a field experiment on plant–soil interactions with 20 plant species I specifically asked: Does aboveground herbivory impact root morphological traits of plants?

Methods

Field experiment

The impact of aboveground herbivory on root morphological traits was tested within the scope of an experiment on plant–soil interactions conducted in a meadow at a field site of the University of Potsdam (N52° 24' 29.76", E13° 1' 13.74", Brandenburg, Germany; see Heinze et al. 2016; Heinze and Joshi 2018). The soil in this meadow consists of nutrient poor slightly sandy loam (pH: 6–7) and the plant community has high diversity (> 60 species).

The design of this experiment has been described elsewhere (Heinze et al. 2020). Briefly, under field conditions we tested whether aboveground herbivory affects the outcome of plant–soil feedbacks (PSFs) for 20 grassland species [10 grasses and 10 forbs (including three legumes); see Fig. 1]. Therefore, growth with and without aboveground insect herbivores of these 20 plant species was tested in soils previously conditioned by themselves (i.e., home soil) as well as by the remaining 19 species (i.e., away soil) collected in the meadow. For each species there was one home soil and one away soil. The away soil was created by mixing equal portions of each of the other 19 species. Potential differences in soil nutrient availability among soils were avoided by inoculating home and away soils (10%) into an autoclaved soil:sand mixture (five times within 24 h; 20 min, 121 °C). The home and away soils for every species did not differ in plant-available (Heinze et al. 2020) nor total nutrient concentrations (see Online Resource Table S1). In this experiment plants were grown in the meadow in buried (depth: 25 cm) pots (Deepots D25L; Stuewe & Sons; USA) to enable a standardized soil volume for root growth. To test single-plant responses, one individual was planted per pot. The pots were distributed over 10 paired plots equipped with cages which were either completely covered with fly mesh (– herbivory; mesh size: 1.3 mm; Meyer; Germany) or only shaded (+ herbivory; no fly mesh at the lower 50 cm) to prevent potential differences in shade or precipitation. Each ‘species by soil’ combination was replicated 10 times within each herbivory treatment (i.e., + or – herbivory), resulting in 800 pots (20 species × 2 soils × 2 herbivory treatments × 10 replicates). Plants were grown for 12 weeks in summer 2017.

This study tests and reports the effects of aboveground insect herbivory on plants and their root morphological traits for three randomly chosen replicates per species, soil and herbivory treatment (i.e., 240 samples) to directly link herbivory damage with changes in root morphology.

Measurements

Before harvest, damage by chewing and leaf mining insect herbivores was visually assessed without any further discrimination of feeding guilds. Grasshoppers represent the most important herbivores in this

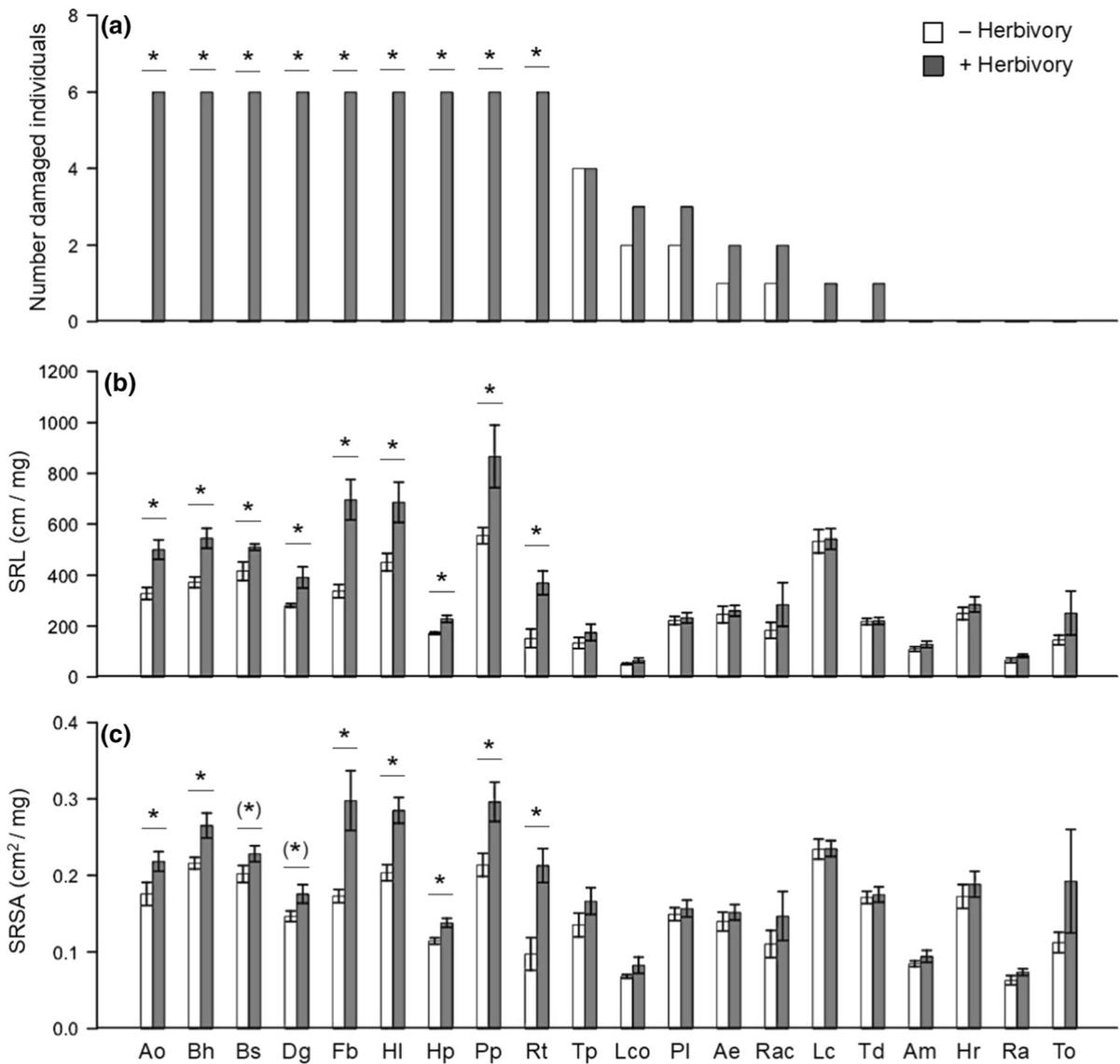


Fig. 1 Number damaged individuals (a), specific root length (SRL, b) and specific root surface area (SRSA, c) of 20 plant species grown without (white bars) and with (gray bars) aboveground insect herbivores. In a data represent sums of damaged individuals and in b and c mean \pm SE ($n = 6$). In a asterisks above two bars indicate significant differences after Fisher’s exact tests and in b and c after t -test analysis: $*P < 0.05$; $*P < 0.1$. Species abbreviations are as follows: Ao, *Anthoxanthum odoratum*; Bh, *Bromus hordeaceus*; Bs,

Bromus sterilis; Dg, *Dactylis glomerata*; Fb, *Festuca brevipila*; Hl, *Holcus lanatus*; Hp, *Helictotrichon pubescens*; Pp, *Poa pratensis*; Rt, *Rumex thyrsiflorus*; Tp, *Trifolium pratense*; Lco, *Lotus corniculatus*; Pl, *Plantago lanceolata*; Ae, *Arrhenatherum elatius*; Rac, *Rumex acetosella*; Lc, *Luzula campestris*; Td, *Trifolium dubium*; Am, *Achillea millefolium*; Hr, *Hypochaeris radicata*; Ra, *Ranunculus acris*; To, *Taraxacum officinale*

grassland (see Heinze and Joshi 2018; Heinze et al. 2020). Biomass removal was visually estimated (in percent severity; see also, e.g., Johnson et al. 2016b) at ten randomly chosen leaves per individual plant. Furthermore, the proportion of damaged leaves was

determined by counting the number of damaged as well as total leaves (incidence) on each experimental plant (see Russell et al. 2010). Severity and incidence were subsequently used to assess the shoot biomass removal by aboveground insect herbivores for whole

experimental plants according to Smith et al. (2005). Information on whether a plant's leaves showed any damage, or not, was used to categorize the damage status of individual plants (damaged vs. undamaged) to test whether herbivore damage affected root morphological traits.

After herbivory measurements, shoots were harvested and roots were washed. To determine root length and diameter, a representative subsample of the whole root system (max diameter: 0.47 mm) of each plant was analyzed using the WinRhizo scanner-based system (Regents Instruments, Inc., Canada). Afterward, roots (i.e., the representative subsample of the whole root system and the remaining roots per individual) were dried (48 h, 80 °C) and weighed to obtain root mass. The biomass of the representative subsamples was used to calculate specific root morphological traits (except average diameter, AD) according to Ryser and Lambers (1995) and Wright and Westoby (1999): specific root length (SRL; cm/mg), specific root surface area (SRSA; cm²/mg) and root tissue density (RTD; mg/cm⁻³).

Statistical analysis

All analyses were performed in R version 3.1.2 (R Developmental Core Team 2014). Before analyses residuals were checked for homogeneity of variance and tested for normality.

In addition to shoot biomass removal, I used a plant's damage status (damaged vs. undamaged) as a response variable in analyses. I made this decision because plant responses to insect herbivory are very sensitive, i.e., signals from few injured cells are sufficient to induce physiological responses (Howe and Jander 2008) including changes in phytohormones that affect root development and morphology.

To test whether aboveground herbivory (i.e., – herbivory and + herbivory) impacts the number of damaged individuals, shoot biomass removal, root biomass and root morphological traits of plants I performed ANOVAs using generalized linear mixed models (lme4 package; Bates et al. 2015). Block (i.e., replicate) was included as random factor. *P*-values and degrees of freedom were estimated with Type III Kenward–Roger approximation using lmerTest (Kuznetsova et al. 2017). As this experiment also tested the effects of soils (i.e., home and away) that possibly generate differences in damage by aboveground

herbivores (Heinze et al. 2019), the models included the factors 'species,' 'soil' and 'herbivory' as well as their interactions. Afterward, differences in shoot biomass removal, root biomass and root morphological traits between presence and absence of herbivores were tested using two sample *t*-tests for every species. Differences between functional groups (i.e., grasses vs. forbs) were tested by replacing 'species' by 'functional group' in the models and using 'species' nested in 'functional group' as additional random factor.

Because the data on plant damage status followed a binomial distribution I used the glmer-function with binomial error distribution and Fisher's exact tests as post hoc tests to evaluate species-specific differences in number of damaged individuals between the— and + herbivory plots.

Results

Different soils (home vs. away) affected the amount of biomass removal by herbivorous insects, but not the number of damaged individuals, root biomass and root morphological traits tested (see Table S2). The 'Results' section therefore focuses on effects of aboveground insect herbivory and in the figures the data for the two soils are combined.

Herbivory effects on individuals of the 20 species

The presence/absence of aboveground insect herbivores affected the number of damaged individuals and the intensity of shoot biomass removal differently for the functional groups as well as for the 20 plant species (functional group/species × herbivory interaction: *P* < 0.001 for shoot removal and number damaged plants; see Online Resource Table S2). For 8 grass and 1 forb species, all individuals were damaged and showed substantial shoot biomass removal when grown with herbivores, but suffered no shoot damage when grown without herbivores (Fig. 1a; Online Resource Fig. S1). The remaining species showed little shoot damage (Online Resource Fig. S1). Individuals of these species either were not damaged or were equally damaged in the + and – herbivory plots because the herbivore exclusion was ineffective for a few species (Fig. 1a).

Herbivory effects on root biomass and root morphological traits

Aboveground herbivores influenced root biomass and root morphological traits but only for those 8 grass and 1 forb species for which the herbivory exclusion manipulation significantly altered number damaged individuals and amount of herbivore damage (species \times herbivory interaction: root biomass: $F_{19,160} = 4.14$; $P < 0.001$; SRL: $F_{19,160} = 3.30$; $P < 0.001$; SRSA: $F_{19,160} = 2.06$; $P = 0.009$; Fig. 1b, c, Online Resource Table S2, Fig. S2a) or for subsets of these 9 species (AD: $F_{19,160} = 2.49$; $P = 0.024$; RTD: $F_{19,160} = 2.58$; $P < 0.001$; Online Resource Table S2, Fig. S2b, c). For these species root biomass, SRL and SRSA increased, whereas AD and RTD decreased when individuals showed damage by aboveground herbivores (Fig. 1b, c and Online Resource Fig. S2). In contrast, root biomass and morphological traits for species whose individuals were either equally damaged in the + and – herbivory plots or not damaged showed no differences (Fig. 1b, c and Online Resource Fig. S2).

Discussion

In accordance with previous studies, damaged plants in this experiment showed an increase in root biomass with aboveground herbivory (McNickle and Evans 2018; Sarquis et al. 2019). However, more importantly, aboveground herbivory increased SRL and SRSA, but only for the 8 grass and 1 forb species for which herbivory exclusion significantly reduced herbivore damage. For one species tested in this experiment, *Poa pratensis*, Thorne and Frank (2009) also observed an increase in SRL after aboveground biomass removal by clipping. Several studies involving other species, however, found no impact of biomass removal on root morphological traits (Pastore and Russell 2012; Leuschner et al. 2013; Tiiva et al. 2019). An increase in SRL and most likely SRSA is presumably associated with an increase in soil resource uptake efficiency (Thorne and Frank 2009). Hence, a change of root morphological traits under herbivory towards thinner roots with increased specific root surface might increase nutrient uptake to compensate for aboveground biomass loss.

That grasses responded more strongly to the herbivory manipulation compared to forbs might be due to the fact that in this system grasshoppers are the main insect herbivores (see Heinze and Joshi 2018; Heinze et al. 2020). Grasshoppers, although being generalist herbivores (Branson and Sword 2009), predominantly feed on grasses (Pfisterer et al. 2003; Franzke et al. 2010). Hence, the high preference of grasshoppers for grasses most likely caused differences in damage between grasses and forbs. However, like in other studies, in this study a few plants showed limited insect herbivore damage in the—herbivory plots, indicating that cage exclusion did not completely prevent damage by all herbivorous insects (see e.g., Palmisano and Fox 1997; Bevill et al. 1999). Nevertheless, herbivory exclusion effectively excluded grasshoppers that caused most damage in plants in the + herbivory plots in this experiment (J. Heinze, personal observation) and therefore most probably impacted root morphological traits.

As root morphological traits are important for the occupation of soil space (Casper and Jackson 1997), uptake processes, decomposition and interactions with soil biota (Bardgett et al. 2014), they have recently gained much attention in the contexts of PSFs (see e.g., Baxendale et al. 2014; Bergmann et al. 2016; Wilschut et al. 2019) and plant–plant competition (e.g., Ravenek et al. 2016; Semchemko et al. 2018). Hence, aboveground herbivory effects on morphological root traits might be relevant for two important research fields in plant ecology.

Potential effects on PSFs and plant–plant competition

Thinner roots with a lower RTD (i.e., lower investment in dry matter; see Ryser 1996) are likely to decompose faster than roots with high diameter and RTD and thus might impact root-litter mediated PSFs (DeLong et al. 2019; Veen et al. 2019). Furthermore, root systems with a higher SRL and SRSA will also have a higher susceptibility for pathogen infection and root herbivory (Newsham et al. 1995), potentially leading to an accumulation of negative PSFs (Kulmatiski et al. 2008). In addition, a higher specific root surface enables plants to absorb more water and nutrients, which might increase competition for limiting resources between plants and soil biota (Gustafson and Casper 2004; Manning et al. 2008) and thus

potentially impact the composition of soil microbial communities involved in PSFs.

Plants with larger and more finely branched root systems absorb more limiting resources (e.g., nutrients, water) and occupy more soil space and thus are more competitive, compared to plants with large diameter roots (Ravenek et al. 2016), although the outcome of competition also depends on the spatial distribution of the resources and resource-acquiring organs (Schenk 2006). However, in general, large and well-proliferated root systems are particularly important for establishing aboveground dominance (Frank et al. 2010).

Although this study reveals important findings with implications for two important fields in plant ecology there are several unresolved issues. For example, it remains unknown whether damage type (e.g., mowing/clipping, herbivory), herbivore type (e.g., ungulates, snails, insects) or feeding type (chewing, sucking, mining) differently impact root morphological traits. Furthermore, because root morphological traits inherently act together with all other root traits, such as physiological or biotic root traits (Bardgett et al. 2014), their relative importance to feedback and competition processes may be difficult to assess.

Taken together, this study shows that aboveground herbivory impacts root morphological traits of plants, and suggests that herbivory-induced changes in root morphology might be important for the outcome of PSFs and plant–plant competition.

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Author contributions JH conceived the idea, designed the study, performed the experiment, collected and analyzed the data and wrote the manuscript.

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References

- Branson DH, Sword GA (2009) Grasshopper herbivory affects native plant diversity and abundance in a grassland dominated by the exotic grass *Agropyron cristatum*. *Restor Ecol* 17:89–96. <https://doi.org/10.1111/j.1526-100x.2007.00343.x>
- Bardgett RD, Wardle DA, Yeates GW (1998) Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biol Biochem* 30:1867–1878. [https://doi.org/10.1016/S0038-0717\(98\)00069-8](https://doi.org/10.1016/S0038-0717(98)00069-8)
- Bardgett RD, Mommer L, de Vries FT (2014) Going underground: root traits as drivers of ecosystem processes. *Trends Ecol Evol* 29:692–699. <https://doi.org/10.1016/j.tree.2014.10.006>
- Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1–48
- Baxendale C, Orwin KH, Poly F, Pommier T, Bardgett RD (2014) Are plant–soil feedback responses explained by plant traits? *New Phytol* 204:408–423. <https://doi.org/10.1111/nph.12915>
- Bergmann J, Verbruggen E, Heinze J, Xiang D, Chen B, Joshi J, Rillig MC (2016) The interplay between soil structure, roots, and microbiota as a determinant of plant–soil feedback. *Ecol Evol* 6:7633–7644. <https://doi.org/10.1002/ece3.2456>
- Bevill RL, Louda SM, Stanforth LM (1999) Protection from natural enemies in managing rare plant species. *Conserv Biol* 13:1323–1331
- Bezemer TM, van Dam NM (2005) Linking aboveground and belowground interactions via induced plant defenses. *Trends Ecol Evol* 20:617–624. <https://doi.org/10.1016/j.tree.2005.08.006>
- Casper BB, Jackson RB (1997) Plant competition underground. *Annu Rev Ecol Syst* 28:545–570. <https://doi.org/10.1146/annurev.ecolsys.28.1.545>
- Crawley MJ (1989) Insect herbivores and plant population dynamics. *Annu Rev Entomol* 34:531–564. <https://doi.org/10.1146/annurev.en.34.010189.002531>
- DeLong JR, Fry EL, Veen GF, Kardol P (2019) Why are plant–soil feedbacks so unpredictable, and what to do about it? *Func Ecol* 33:118–128. <https://doi.org/10.1111/1365-2435.13232>
- Frank DA, Pontes AW, Maine EM, Caruana J, Raina R, Raina S, Fridley JD (2010) Grassland root communities: species distributions and how they are linked to aboveground

- abundance. *Ecology* 91:3201–3209. <https://doi.org/10.1890/09-1831.1>
- Franzke A, Unsicker SB, Specht J, Köhler G, Weisser WW (2010) Being a generalist herbivore in a diverse world: how do diets from different grasslands influence food plant selection and fitness of the grasshopper *Chorthippus parallelus*? *Ecol Entomol* 35:126–138. <https://doi.org/10.1111/j.1365-2311.2009.01168.x>
- Gustafson DJ, Casper BB (2004) Nutrient addition affects AM fungal performance and expression of plant/fungal feedback in three serpentine grasses. *Plant Soil* 259:9–17. <https://doi.org/10.1023/B:PLSO.0000020936.56786.a4>
- Heinze J, Sitte M, Schindhelm A, Wright J, Joshi J (2016) Plant-soil feedbacks: a comparative study on the relative importance of soil-feedbacks in the greenhouse vs. field. *Oecologia* 181:559–569. <https://doi.org/10.1007/s00442-016-3591-8>
- Heinze J, Joshi J (2018) Plant-soil feedback effects can be masked by aboveground herbivory under natural field conditions. *Oecologia* 186:235–246. <https://doi.org/10.1007/s00442-017-3997-y>
- Heinze J, Simons NK, Seibold S, Wacker A, Weithoff G, Gossner MM, Prati D, Bezemer TM, Joshi J (2019) The relative importance of plant-soil feedbacks for plant-species performance increases with decreasing intensity of herbivory. *Oecologia* 190:651–664. <https://doi.org/10.1007/s00442-019-04442-9>
- Heinze J, Wacker A, Kulmatiski A (2020) Plant-soil feedback effects altered by aboveground herbivory explain plant species abundance in the landscape. *Ecology*. <https://doi.org/10.1002/ecy.3023>
- Howe GA, Jander G (2008) Plant immunity to insect herbivores. *Annu Rev Plant Biol* 59:41–66. <https://doi.org/10.1146/annurev.arplant.59.032607.092825>
- Johnson SN, Erb M, Hartley SE (2016a) Roots under attack: contrasting plant responses to below- and aboveground insect herbivory. *New Phytol* 210:413–418. <https://doi.org/10.1111/nph.13807>
- Johnson MTJ, Bertrand JA, Turcotte MM (2016b) Precision and accuracy in quantifying herbivory. *Ecol Entomol* 41:112–121. <https://doi.org/10.1111/een.12280>
- Karolewski P, Zadworny M, Mucha J, Napierala-Filipiak A, Oleksyn J (2010) Link between defoliation and light treatments on root vitality of five understory shrubs with different resistance to insect herbivory. *Tree Physiol* 30:969–978. <https://doi.org/10.1093/treephys/tqp060>
- Kulmatiski A, Beard KH, Stevens JR, Cobbold SM (2008) Plant-soil feedbacks: a meta-analytic review. *Ecol Lett* 11:980–992. <https://doi.org/10.1111/j.1461-0248.2008.01209.x>
- Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest: tests in linear mixed effects models. *J Stat Softw* 82:1–26
- Lee S, Sergeeva LI, Vreughenhil D (2018) Natural variation of hormone levels in Arabidopsis roots and correlations with complex root architecture. *J Int Plant Biol* 60:292–309. <https://doi.org/10.1111/jipb.12617>
- Leuschner C, Gebel S, Rose L (2013) Root trait responses of six temperate grassland species to intensive mowing and NPK fertilization: a field study in a temperate grassland. *Plant Soil* 373:687–698. <https://doi.org/10.1007/s11104-013-1836-4>
- Lymperopoulos P, Msanne J, Rabara R (2018) Phytochrome and phytohormones: working in tandem for plant growth and development. *Front Plant Sci* 9:1037. <https://doi.org/10.3389/fpls.2018.01037>
- Manning P, Morrison SA, Bonkowski M, Bardgett RD (2008) Nitrogen enrichment modifies plant community structure via changes to plant-soil feedback. *Oecologia* 157:661–673. <https://doi.org/10.1007/s00442-008-1104-0>
- Maron JL, Crone E (2006) Herbivory: effects on plant abundance, distribution and populations growth. *Proc R Soc B* 273:2575–2584. <https://doi.org/10.1098/rspb.2006.3587>
- Maron JL (1998) Insect herbivory above- and belowground: individual and joint effects on plant fitness. *Ecology* 79:1281–1293. [https://doi.org/10.1890/0012-9658\(1998\)079\[1281:IHAABI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[1281:IHAABI]2.0.CO;2)
- McNickle GG, Evans WD (2018) Toleration games: compensatory growth by plants in response to enemy attack is an evolutionarily stable strategy. *AoB Plants* 10:ply035. <https://doi.org/10.1093/aobpla/ply035>
- Newsham KK, Fitter AH, Watkinson AR (1995) Multi-functionality and biodiversity in arbuscular mycorrhizas. *Trends Ecol Evol* 10:407–411. [https://doi.org/10.1016/S0169-5347\(00\)89157-0](https://doi.org/10.1016/S0169-5347(00)89157-0)
- Palmisano S, Fox LR (1997) Effects of mammal and insect herbivory on population dynamics of a native *Californian thistle*, *Cirsium occidentale*. *Oecologia* 111:413–421. <https://doi.org/10.1007/s004420050253>
- Pfisterer A, Diemer M, Schmid B (2003) Dietary shift and lowered biomass gain of a generalist herbivore in species-poor experimental plant communities. *Oecologia* 135:234–241. <https://doi.org/10.1007/s00443-002-1169-0>
- Pastore AI, Russell FL (2012) Insect herbivore effects on resource allocation to shoots and roots in *Lespedeza capitata*. *Plant Ecol* 213:843–851. <https://doi.org/10.1007/s11258-012-0046-0>
- R Developmental Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ravenek JM, Mommer L, Visser EJW, van Ruijven J, van der Paauw JW, Smit-Tiekstra A, de Caluwe H, de Kroon H (2016) Linking root traits and competitive success in grassland species. *Plant Soil* 407:39–53. <https://doi.org/10.1007/s11104-016-2843-z>
- Russell FL, Rose KE, Louda SM (2010) Seed availability and insect herbivory limit recruitment and adult density of native tall thistle. *Ecology* 91:3081–3093. <https://doi.org/10.1890/09-1101.1>
- Ryser P, Lambers H (1995) Root and leaf attributes accounting for the performance of fast and slow-growing grasses at different nutrient supply. *Plant Soil* 170:251–265. <https://doi.org/10.1007/BF00010478>
- Ryser P (1996) The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses. *Funct Ecol* 10:717–723. <https://doi.org/10.2307/2390506>
- Sarquis A, Pestoni S, Cingolani AM, Harduindeguy NP (2019) Physiognomic changes in response to herbivory increase carbon allocation to roots in a temperate grassland of

- central Argentina. *Plant Ecol* 220:699–709. <https://doi.org/10.1007/s11258-019-00945-w>
- Schenk HJ (2006) Root competition: beyond resource depletion. *J Ecol* 94:725–739. <https://doi.org/10.1111/j.1365-2745.2006.01124.x>
- Semchemko M, Lepik A, Abakumova M, Zobel K (2018) Different sets of belowground traits predict the ability of plant species to suppress and tolerate their competitors. *Plant Soil* 424:157–169. <https://doi.org/10.1007/s11104-017-3282-1>
- Smith AH, Pinkard EA, Stone C, Battaglia M, Mohammed CL (2005) Precision and accuracy of pest and pathogen damage assessment in young Eucalytus plantations. *Environ Monit Assess* 111:243–256. <https://doi.org/10.1007/s10661-005-8222-5>
- Thorne MA, Frank DA (2009) The effects of clipping and soil moisture on leaf and root morphology and root respiration in two temperate and two tropical grasses. *Plant Ecol* 200:205–215. <https://doi.org/10.1007/s11258-008-9445-7>
- Tiiva P, Julkunen-Tiitto R, Häikiö E, Kasurinen A (2019) Belowground responses of scots pine (*Pinus sylvestris*) seedlings to experimental warming, moderate nitrogen addition, and bark herbivory. *Can J For Res* 49:647–660. <https://doi.org/10.1139/cjfr-2018-0099>
- Veen GF, Fry E, ten Hooven F, Kardol P, Morrien E, DeLong JR (2019) The role of plant litter in driving plant-soil feedbacks. *Front Environ Sci* 7:168. <https://doi.org/10.3389/fenvs.2019.00168>
- Wilschut RA, van der Putten WH, Garbeva P, Harkes P, Konings W, Kulkarni P, Martens H, Geisen S (2019) Root traits and belowground herbivores relate to plant-soil feedback variations among species. *Nat Commun* 10:1564. <https://doi.org/10.1038/s41467-019-09615-x>
- Wright IJ, Westoby M (1999) Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients. *J Ecol* 87:85–97. <https://doi.org/10.1046/j.1365-2745.1999.00330.x>

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