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Legacy effects of herbivory enhance performance and resistance of progeny plants

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Abstract

1. Herbivory-induced changes in plant resistance and tolerance traits can mediate the interaction between spatially and temporally separated above- and below-ground herbivores. However, it is unknown how long the impact of transient herbivory events last or if legacy effects can be detected systemically in the plant and across plant generations.
2. Here, we studied the impact of transient above-ground herbivory by the specialist caterpillar *Manduca sexta* on the plant traits of wild tobacco *Nicotiana attenuata* and the consequences for below-ground root-knot nematodes *Meloidogyne incognita* in short-term, long-term, and transgenerational experiments.
3. In the short- and long-term experiments, above- and below-ground herbivory had significant, albeit independent, impacts on key plant traits such as plant biomass, nutrient content, and secondary metabolites. In addition, herbivory influenced fitness parameters such as seed yield and quality. In the long-term and transgenerational experiments, transient above-ground herbivory had facilitating effects on nematodes, irrespective of any treatments of the parental plants. We found evidence for transgenerational legacy effects of both above- and below-ground herbivory on the resistance of progeny plants against above-ground herbivores. Additionally, below-ground herbivory in the parental generation increased the root biomass of progeny plants.
4. *Synthesis*. Our results suggest that herbivory may have a long-term impact on plant fitness by improving the performance of progeny plants challenged by above- and below-ground herbivory.

KEYWORDS

above- and below-ground interactions, legacy effects, plant defence, plant fitness, plant–herbivore interactions, priming, tolerance, transgenerational priming

1 | INTRODUCTION

Roots are challenged by a multitude of herbivores, but most herbivory studies have focused on above-ground plant–herbivore interactions. Over the past decade, increasing research has been carried out to analyse the ecological and molecular aspects of below-ground plant–herbivore interactions (e.g., Erb, Glauser, & Robert, 2012), in addition to going a step further by analysing plant-mediated indirect interactions between above- and below-ground herbivores (e.g., Soler et al., 2007; Wurst & van der Putten, 2007). It has been shown that above-ground herbivores may affect the performance of belowground herbivores via herbivore-induced systemic changes in defensive compounds (e.g., Huang, Siemann, Xiao, Yang, & Ding, 2014; Li et al., 2016; Soler et al., 2007) or in plant nutritional resources (e.g., Kaplan et al., 2008). However, the majority of the research has focused on the effects of below-ground herbivory on above-ground herbivores and has considered the spatial rather than temporal separation of herbivores. Recently, it has been suggested that herbivore-induced changes in plant traits and soil characteristics may persist even after the herbivores are gone, which may therefore affect temporarily separated, subsequent herbivores, a phenomenon that is called legacy effect (Kostenko, Voorde, Mulder, Putten, & Bezemer, 2012; Wurst & Ohgushi, 2015). For example, Barber, Adler, Theis, Hazzard, and Kiers (2012) showed that cucumber *Cucumis sativus* plants treated with high levels of above-ground herbivorous cucumber beetles *Acalymma vittatum* in early season were less susceptible to subsequent above- and below-ground herbivory by conspecifics in late season. Similarly, Kostenko et al. (2012) showed that the legacy effect of previous above- and below-ground herbivory on the soil fungal community resulted into altered plant characteristics and plant–herbivore interactions in succeeding plant generations. However, so far it is largely unknown how long the legacy effects of transient herbivory last and if they can be detected systemically in the plant and across plant generations.

Furthermore, effects of transient herbivory on plants may differ during plant ontogeny and with the time passed since the herbivory event. For instance, younger plants invest their resources in growth and development, while mature plants invest in reproduction; thus, defensive strategies may also vary with age (Barton & Koricheva, 2010; Boege & Marquis, 2005) as well as the time passed since the herbivory event (Hilker et al., 2016). Therefore, the effect of transient herbivory on plant traits can be expected to depend both on the time passed since the herbivory event and the developmental stage of the plant. In this paper, we focus on the effect of transient above-ground herbivory experienced by plants in an early developmental stage on plant traits in the following developmental stages: vegetative growth, reproduction, and progeny generation. Furthermore, we investigate the consequences of above-ground herbivore-induced systemic changes in plant traits for the performance of subsequent below-ground herbivores.

Generally, the outcome of plant-mediated herbivore interactions may be facilitative, detrimental, or neutral to herbivores. The effects may depend on several factors such as plant type and their defence strategy, identity, feeding guild, and sequence of arrival of the herbivores (Bezemer, Wagenaar, Dam, & Wackers, 2003; Erb, Robert, Hibbard, & Turlings, 2011; Johnson et al., 2012; Kaplan et al., 2008; Kutyniok & Müller, 2013; Wurst & van der Putten, 2007; Wurst, Dam, Monroy, Biere, & Putten, 2008). Several studies have shown that above-ground herbivores are more likely to have antagonistic effects on below-ground herbivores when they arrive first on the plant (Erb et al., 2011; Johnson et al., 2012). Early arrival on the host plant may be associated with a competitive advantage for the “early birds” because they forage naïve plants with minimal defence and may eventually induce local and systemic plant responses with potential negative effects on latecomers. Thereby, such sequential herbivory events may even result in priming of the plant, that is, earlier herbivory prepares the plant for a better or quicker response upon subsequent herbivory (Conrath et al., 2006; Frost, Mescher, Carlson, & Moraes, 2008; Hilker et al., 2016).

In addition to priming within a single generation, parental plants, based on the cues of stress events experienced in their generation, may differentially endow their offspring with changes in phenotype so as to withstand potential stresses through the process of transgenerational induction or priming (Agrawal, Laforsch, & Tollrian, 1999; Holeski, Jander, & Agrawal, 2012; Rasmann et al., 2012; Verhoeven & van Gurp, 2012). For example, in one of the earliest studies on transgenerational effects to be conducted in an above-ground context, Agrawal et al. (1999) found that wild radish *Raphanus raphanistrum* plants whose parents were exposed to specialist caterpillars *Pieris rapae* were more resistant against conspecific caterpillars when compared to the progeny of undamaged parents. Primarily, two mechanisms are suggested for such effects: maternal effects, such as seed provisioning, and/or epigenetic effects, such as DNA methylation and mobile small RNA (Chitwood & Timmermanns, 2010; Holeski et al., 2012). Since this is a relatively new topic in the field of ecology, the adaptive value (i.e., fitness consequences) and the mechanisms of the transgenerational effects are not fully understood. Furthermore, priming by herbivores has not been shown in an above-belowground context, that is, involving both shoot and root herbivores.

In this study, we examined how long the legacy effects of transient above-ground herbivory in an early developmental stage of the plant last and if they can be detected in later developmental stages and even across plant generations. To test our hypotheses, we used wild tobacco (*Nicotiana attenuata* Torr. Ex Watson, Solanaceae) as a model plant and the specialist chewing caterpillar *Manduca sexta* (Sphingidae) and the generalist root-knot nematode *Meloidogyne incognita* (Heteroderidae) as above- and below-ground herbivores, respectively. We tested the following hypotheses by conducting short-term, long-term, and transgenerational experiments (Supporting Information Figure S1) that focused on the vegetative growth stage, the reproductive stage, and the progeny generation, respectively: (a) Earlier transient above-ground herbivory induces systemic changes in plant traits that will adversely affect the performance of subsequent below-ground herbivores; (b) effects of transient above-ground herbivory persist for long enough to have an impact on the lifetime fitness of plants, such as seed production; and (c) above- and below-ground herbivory in the parental plants increase the resistance of the progeny plants to herbivory via transgenerational priming responses. Since all the existing scientific studies on transgenerational priming/induction have been conducted in an above-ground context, our study is the first to take the systemic impacts of both above- and below-ground herbivores into account. This is a crucial next step, since plants in natural environments are challenged by herbivores both above and below the ground.

2 | MATERIALS AND METHODS

2.1 | Plant

Nicotiana attenuata is an annual wild tobacco native to the southwestern United States (Baldwin & Ohnmeiss, 1993). Several studies have confirmed that *N. attenuata* induces defence compounds such as nicotine and protease inhibitors and produces volatile compounds upon leaf herbivory (Baldwin, Gorham, Schmelz, Lewandowski, & Lynds, 1998; Kessler & Baldwin, 2001; van Dam, Horn, Mares, & Baldwin, 2001). Since the defensive alkaloid nicotine is known to be biosynthesized in the roots of tobacco plants as a response to shoot herbivory (Baldwin, 1989), it is an interesting model plant for studying the interaction between above- and below-ground herbivores. Wild type *N. attenuata* seeds, obtained from the 17th inbred line originating at the Great Basin Desert, Utah, USA (Baldwin, 1998), were used for the short- and long-term experiments, while the seeds of the plants from the long-term experiment were used in the transgenerational experiment. Seeds were surface sterilized and germinated on Gamborg's B5 medium, as explained in Krügel, Lim, Gase, Halitschke, and Baldwin (2002). Eight-day-old seedlings were transferred to seedling trays. After growing in seedling trays for 12 days, healthy and homogeneous plants were transferred to 2.5 L (16 cm diameter, 16 cm height) plastic pots (Pöppelmann GmbH and Co. KG, Lohne, Germany) containing 2.3 L of steamed soil:sand mixture. To obtain this mixture, standard potting soil "type T" (Einheitserdewerke Werkverband e. V., Sinntal-Altengronau, Germany) was mixed with fine sand in a ratio of 3:2 (soil:sand by volume). The mixture was steamed for 3 hours at 90°C using a Sterilo steamer (Harter Elektrotechnik, Schenkenzell, Germany) in order to exclude root herbivores. Pots were placed on individual plastic plates and the top layer of the soil was covered with sand grit so as to prevent the growth of green algae and infestation of fungus gnats (Sciaridae). Plants were randomized weekly to homogenize for variances due to abiotic factors such as light conditions.

2.2 | Herbivores

Tobacco hornworm *M. sexta* is a specialist herbivore feeding on plants of the Solanaceae family, including *N. attenuata*. The larvae of *M. sexta* were obtained from the laboratory cultures maintained at the Department of Applied Zoology, Freie Universität Berlin. They were reared on an artificial diet (a wheat germ-based basic diet with a vitamin mix) in a climate chamber at 24°C and 70% humidity under a 16/8-hr day/night light cycle. Root-knot nematode, *M. incognita*, is a globally distributed plant parasite that feeds on the roots of numerous host plants, including commercial tobacco *Nicotiana tabacum* (Barker, 2003; Koenning et al., 1999), in addition to being found in the natural habitat of *N. attenuata* plants (R. Machado, personal communication). Second-stage juveniles (J2s) of *M. incognita* (nematode hereafter) were obtained from a biological supply company (Hettema Zaaizaad en Pootgoed Coöperatie [HZPC Holland B.V.], Metslawier, the Netherlands).

2.3 | Short-term experiment

In the first full factorial experiment (see Supporting Information Figure S1), a total of sixty 6-week-old healthy plants were selected. Half of the plants were treated with above-ground herbivore *M. sexta* (caterpillar hereafter), where a third instar larva was added in a mesh bag and allowed to feed on the youngest, fully expanded leaf for 2 days. Then, a new larva was added onto the second youngest, fully expanded leaf for another 2 days, and a third larva was allowed to feed on the third youngest, fully expanded leaf for 1 day. This way, larvae fed on three consecutive leaves for a total of 5 days. The other half of the plants did not receive caterpillars. After the removal of the caterpillars, the plants were kept for a lag phase of 5 days without any herbivores. Then, second-stage juveniles of *M. incognita* were added to the roots of half of the caterpillar-treated plants and half of the untreated plants, at a density of 3,000 nematodes per pot. Finally, there were four treatments: control (Ctrl), caterpillar only (Cat), nematode only (Nem), and caterpillar followed by the nematode (Cat + Nem), with 15 replicates each. Plant parasitic nematodes such as *M. incognita* may have a patchy distribution in soil (McSorley, 1998). Hence, nematodes may take a considerable amount of time for dispersal and infection of new plants, as the movement of organisms in the soil is relatively slow compared to organisms above-ground. Therefore, it is possible that nematodes infest plants that have already been damaged by above-ground herbivores. In the short-term experiment, the plants were harvested 18 days after the nematode inoculation, when they were still in the vegetative growth stage. Leaf and root subsamples were collected to analyse the nicotine content. To assess the nematode performance following caterpillar feeding, we estimated the population growth of the nematodes by counting the number of nematode galls. The number of galls induced by the nematodes was counted in three different size classes (<1 mm, 1–2 mm, and > 2 mm) after keeping them submerged in water on a tray. Then, the root and shoot materials were dried in an oven at 55°C for 3 days before measuring the dry mass.

2.4 | Long-term experiment

To test the long-term effect of the transient caterpillar herbivory on the reproductive stage of the plants and nematodes, a full factorial experiment similar to the short-term experiment was carried out in parallel. In this long-term experiment, plants (and nematodes) were harvested only after seed production. Thus, plants were kept for 90 days instead of 18 days after nematode inoculation, until the ripened seed capsules were produced (Supporting Information Figure S1). By this time, the nematodes had also reproduced and laid eggs in egg masses on/around the galls. The plants were harvested to count seed capsules, number of galls, and egg masses on the root. The number of egg masses was counted to assess the reproductive success of the nematodes following transient caterpillar feeding. Fifteen fully ripened seed capsules were collected from each plant, and seeds were counted with the help of the image processing program ImageJ (National Institutes of Health, Bethesda, MD, USA) in order to estimate the average number of seeds per capsule. Seeds were threshed from all capsules to measure total seed yield. A small volume of seeds was weighed, and the total number of seeds in this volume were counted using ImageJ to calculate the individual seed mass. Root and shoot biomasses were measured as described in the short-term experiment.

2.5 | Transgenerational experiment

The seeds collected from the plants in the long-term experiment were germinated separately, according to the treatments, their respective parents received: 40 seeds from each parental treatment, totalling 160 plants. Due to the large size of the experiment, seeds were germinated in two blocks separated by 1 day (i.e., two germination blocks). Then, all plants were grown for 6 weeks before the herbivory treatment as in the short- and the long-term experiment (Supporting Information Figure S1). The herbivory treatment was applied on each plant 42 days after its sowing day, that is, the herbivory treatment was also applied in two blocks separated by 1 day. Each progeny group received the identical set of treatments (Ctrl, Cat, Nem, and Cat + Nem) that the parents had received, following the same procedure (Supporting Information Figure S1), resulting in a total of 16 different treatments (four in the parental generation and four in the progeny generation) with 10 replicates each. The individual caterpillar mass was measured before and after the treatment to calculate the mass gain. Plants were harvested on four continuous days (the harvest period) without any bias on the treatments. Plants from the first germination block were harvested on the first and the third day of the harvest period, corresponding to 18 and 20 days after the nematode inoculation. Similarly, plants from the second germination block were harvested on the second and fourth day of the harvest period, also corresponding to 18 and 20 days after the nematode inoculation. The numbers of galls induced by the nematodes were counted in three different size classes, as described in the short-term experiment. Then, the roots and shoots were dried in an oven at 55°C for 3 days before measuring the dry mass.

2.6 | Nicotine measurement

In the short-term experiment, the nicotine content induced by different treatments in the leaf and root tissue of the *N. attenuata* plants was measured by high-performance liquid chromatography (HPLC). The sample extraction procedure for nicotine measurement was modified following Gaquerel, Steppuhn, and Baldwin (2012). In brief, the roots from the harvested plants were washed immediately, and fine roots from five different parts of the root system were collected and mixed together manually. Then, 100–125 mg of these fresh root samples were weighed, placed in 1.5 ml FastPrep tubes, and flash frozen in liquid nitrogen. Similar amounts of leaf samples were taken from the youngest fully expanded rosette leaves. Samples were homogenized using FastPrep homogenizer (FastPrep®-24; MP Biomedicals, Santa Ana, CA, USA). To homogenize the sample, 1 ml of nicotine extraction buffer (40% methanol and 0.5% acetic acid) was added in the FastPrep tube, along with 700 mg of lysing matrix-green (MP Biomedicals) and one 1/4″ Ceramic sphere bead (MP Biomedicals), and then shaken at 6.0 ms^{-1} for 60 s. The supernatant was collected after centrifuging the sample for 10 min at 16,000 *g* at room temperature. The supernatant was centrifuged again to obtain the clean supernatant and stored at −20°C until HPLC analysis. The nicotine contents in the root and shoot tissue were analysed by HPLC (Shimadzu degasser [DGU-20A3], 2x pumps [LC-20AD], diode array detector [SPD-20M20A], controller [CBM-20A], autosampler [SIL 10A], Shimadzu Corp., Kyoto, Japan) following the method described in Keinänen, Oldham, and Baldwin (2001).

2.7 | Carbon and nitrogen concentration measurement

Carbon and nitrogen concentration in the leaf and root tissue of the plants in the short- and long-term experiment were measured in the above- and below-ground plant tissue. Dried leaf and root materials were ground in Eppendorf tubes by using a mixer mill (Mixer Mill MM 400, Retsch GmbH, Haan, Germany) and dried again for at least 24 hr. Then, their carbon and nitrogen concentrations were determined by using an elemental analyser (Euro EA, HEKAtech GmbH, Wegberg, Germany).

2.8 | Statistical analysis

All the statistical analyses were performed using statistical platform “R”, version 3.2.2 (R Development Core Team, 2015). One-way and two-way factorial ANOVAs were performed to test the significance of the herbivory treatments. The data on the number of nematode galls from the long-term experiment were log-transformed in order to meet the assumptions of ANOVA. The individual seed mass data were analysed with GLM, assuming gamma distribution of errors as the data were not normally distributed. Due to the large sample size in the transgenerational experiment, plants were germinated in blocks of 2 days and harvested in blocks of 4 days, ensuring equal distribution of replicates from each treatment for each germination and harvest day. Therefore, the effects of the caterpillar, nematode, and parental treatments on the shoot and root biomass were analysed using linear mixed-effects models. Normally we included the germination and harvest day as random factors, while only the germination day was included as a random factor in the analysis of the parental effect on caterpillar performance on the progeny plants. All the means and *SE*s presented in this paper are unadjusted. All the data are deposited in the Dryad Digital Repository (Kafle & Wurst, 2018).

3 | RESULTS

3.1 | Short-term experiment

3.1.1 | Nematode performance

Transient caterpillar feeding had no significant effect on the number of galls induced by the nematodes in the short-term experiment (Figure 1a).

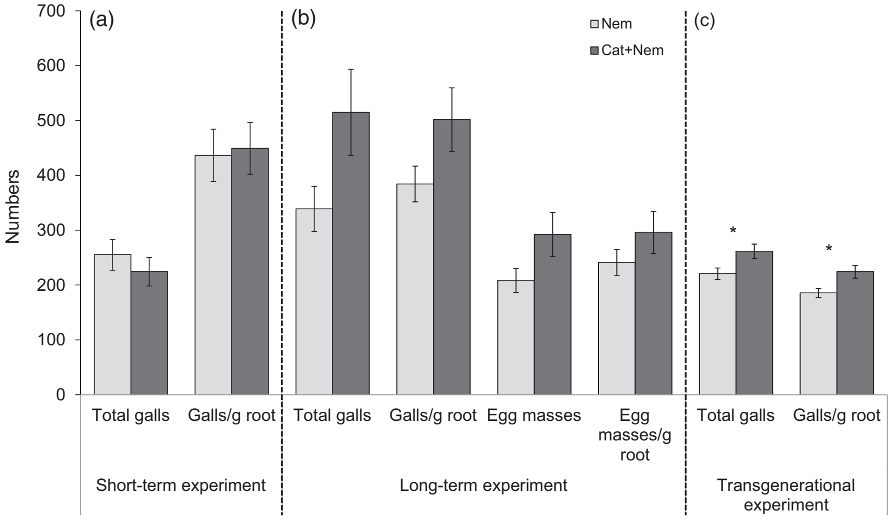

FIGURE 1 Total number of nematode (*Meloidogyne incognita*) galls and total number of galls per unit dry root biomass (mg) induced on plants treated with nematode only (Nem) and caterpillar *Manduca sexta* followed by nematode (Cat + Nem) in the short-term (a), long-term (b), transgenerational experiment (c), and number of egg masses in long-term experiment (b) ($M \pm SE$). An asterisk (*) indicates a significant difference between the mean number of galls at $p < 0.05$. Herbivory treatments in the transgenerational experiment correspond to the treatments in the progeny generation

3.1.2 | Nicotine induction

Neither caterpillar herbivory nor nematode infestation had any effect on the nicotine content in the leaves, while the nematodes induced higher levels of nicotine in the root tissue ($F_{1,55} = 15.76$, $p < 0.001$) independent of the caterpillar feeding (Supporting Information Figure S2).

3.1.3 | Shoot and root biomass

Both shoot and root biomass were significantly reduced by the caterpillar feeding (shoots: $F_{1,56} = 13.48$, $p < 0.001$; roots: $F_{1,56} = 11.61$; $p = 0.001$). The caterpillar herbivory reduced the shoot and root biomass by about 14% each. The nematodes had no effect, and there was no interaction effect (Supporting Information Figures S3a and S4a).

3.1.4 | Carbon and nitrogen concentration

Caterpillar feeding increased the C concentration in the leaf tissue in the short-term experiment. The nematodes significantly altered the C and N concentrations in the root tissue without any changes in their concentrations in the leaves. Nematodes decreased N while increasing C and the C/N ratio in roots (means and statistical test values can be seen in Supporting Information Table S1).

3.2 | Long-term experiment

3.2.1 | Nematode performance

In the long-term experiment, caterpillar herbivory had a marginally positive effect on nematode performance (Figure 1b). The number of galls of the size class bigger than 2 mm were significantly higher in plants previously treated with caterpillars, in comparison to plants treated with nematodes only ($F_{1,18} = 5.343$, $p = 0.033$). Similarly, the total number of galls and total number of galls per g of dry root tissue tended to be higher in plants previously treated with caterpillars (Total galls: $F_{1,18} = 3.664$, $p = 0.072$; Total galls/g root: $F_{1,18} = 3.256$, $p = 0.088$). A similar trend was observed for the total number of egg masses produced by nematodes ($F_{1,18} = 3.288$, $p = 0.087$). The number of egg masses per g of dry root tissue did not differ between treatments ($F_{1,18} = 1.48$, $p = 0.239$).

3.2.2 | Shoot and root biomass

In the long-term experiment, caterpillar feeding had no effect on shoot and root biomass. Below-ground nematode infestation decreased the shoot biomass by approximately 12% ($F_{1,36} = 78.44$, $p < 0.001$) but had no effect on the root biomass (Supporting Information Figure S3b and S4b).

3.2.3 | Carbon and nitrogen concentration

In the long-term experiment, caterpillar feeding had no significant effect on C and N concentrations in the leaf and root tissue of the plants. Nematode herbivory significantly increased both C and N concentrations in the root tissue without any effect on leaf C and N concentrations and the C/N ratio (means and statistical test values can be seen in Supporting Information Table S1).

3.2.4 | Plant fitness

In the long-term experiment, we measured the number of seed capsules, seeds per capsules, total seed yield, and seed characteristics in order to estimate plant fitness. Both caterpillar and nematode herbivory had significant main effects on the number of seed capsules without any interactive effect (caterpillar: $F_{1,36} = 10.34$, $p = 0.002$; nematode: $F_{1,36} = 53.67$; $p < 0.001$). The plants produced about 8% and 17% fewer seed capsules upon herbivory from caterpillar and nematodes, respectively, when compared to the untreated plants (Figure 2a). Despite having a negative impact on the number of seed capsules produced by the plants, the caterpillars increased the number of seeds per capsules

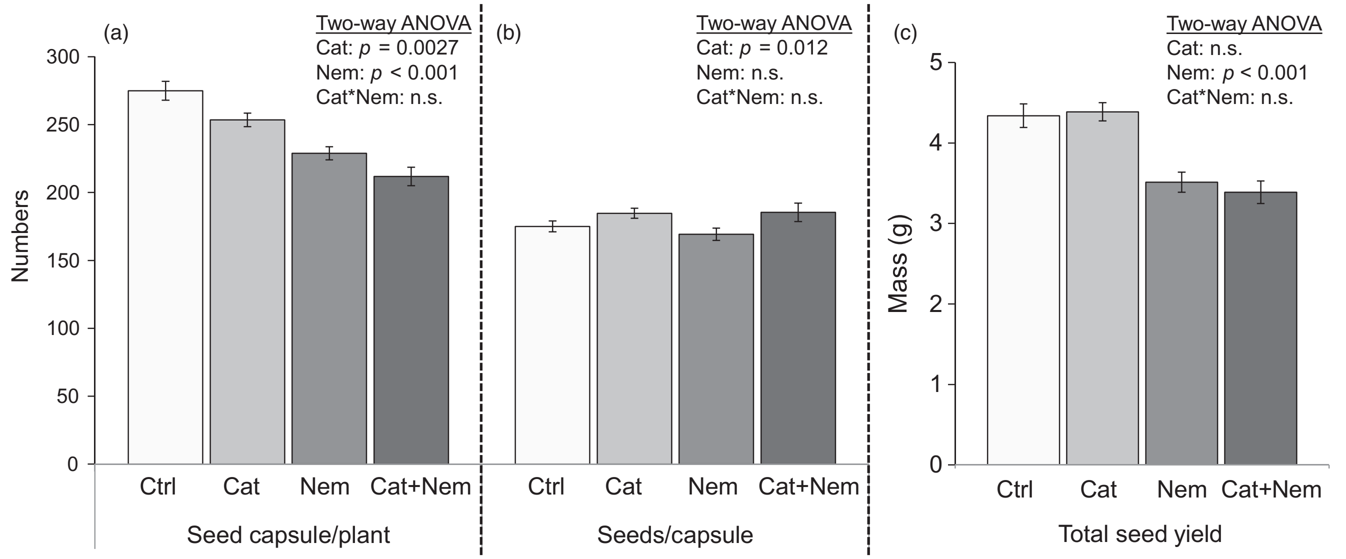

FIGURE 2 Total numbers of seed capsules (a), number of seeds per capsule (b), and total seed yield (g dry mass) (c) of the plants in the long-term experiment (*M* ± *SE*), n.s. stands for not significant. Treatments: Ctrl: control, Cat: Caterpillar only, Nem: Nematode only, and Cat + Nem: Caterpillar followed by nematode herbivory with a lag phase of 5 days

($F_{1,36} = 6.96$, $p = 0.012$) by about 6%, in comparison to the control plants; as a result, total seed yield remained unchanged (Figure 2b,c). The nematodes significantly reduced the total seed yield ($F_{1,36} = 48.17$, $p < 0.001$) by approximately 19%.

The nematodes significantly increased the individual seed mass by about 4% ($F_{1,37} = 4.85$, $p = 0.034$; Supporting Information Figure S5a). There was a main effect of nematodes and an interaction between the caterpillars and the nematodes on the C/N ratio of the seeds (nematode: $F_{1,36} = 4.761$, $p = 0.036$; caterpillar × nematode: $F_{1,36} = 7.918$; $p = 0.008$). Both caterpillars and nematodes interacted to increase the seed C/N ratio, which was even slightly higher than that of the control plants (Supporting Information Figure S5b).

3.3 | Transgenerational experiment

3.3.1 | Caterpillar performance

The sequential herbivory events (caterpillars followed by nematodes) in the parental generation resulted in poor growth of the caterpillar larvae on the progeny plants. The daily mass gain ($F_{1,75} = 7.20$, $p = 0.009$) (Figure 3) and the daily percentage mass gain ($F_{1,75} = 7.64$, $p = 0.007$) (Supporting Information Figure S6) of the caterpillar were both reduced by 6% on the plants whose parents received both the above- and below-ground herbivory (Cat + Nem treatment).

3.3.2 | Nematode performance

The parental treatments had no effect on the performance of the nematodes on progeny plants. However, the above-ground herbivory by the caterpillars in the progeny generation had facilitative effects on nematode performance. The total number of galls and total number of galls per g of the dry root tissue were significantly higher in plants previously treated with caterpillars in the current generation (total galls: $F_{1,69} = 6.568$, $p = 0.013$; total galls/g root: $F_{1,69} = 8.303$, $p = 0.005$) (Figure 1c). Caterpillar-treated plants had about a 19% additional total number of galls when compared to the plants treated with nematodes only. A similar positive effect of the caterpillar feeding was found in the number of galls of size class < 1 mm ($F_{1,69} = 6.595$, $p = 0.012$). This size class comprised the majority (>90%) of the total number of galls. Caterpillar feeding had no effect on the galls of greater size.

3.3.3 | Shoot and root biomass

The parental treatments had no effect on the shoot biomass of the progeny plants, while the caterpillar feeding in the progeny generation had a marginally significant negative effect on total shoot biomass ($F_{1,141} = 3.76$, $p = 0.054$). The nematode herbivory in the progeny generation had no impact on shoot biomass. Nematode herbivory in both the parental and progeny generation had significant main effects on the root biomass (parental nematode treatments: $F_{1,141} = 7.773$, $p = 0.006$; progeny nematode treatment: $F_{1,141} = 7.532$, $p = 0.007$). The nematode herbivory in the progeny generation reduced the root biomass (Figure 4b) by about 5% when compared to the control plants. In contrast, the plant that received the nematode treatment in the parental generation had a higher root biomass (about 4% more when compared to the control plants) in the progeny generation, irrespective of the treatments in the progeny generation (Figure 4a). There was no interaction among any treatments.

4 | DISCUSSION

This study not only confirms that above-ground herbivores may indirectly interact with below-ground herbivores but it also shows that

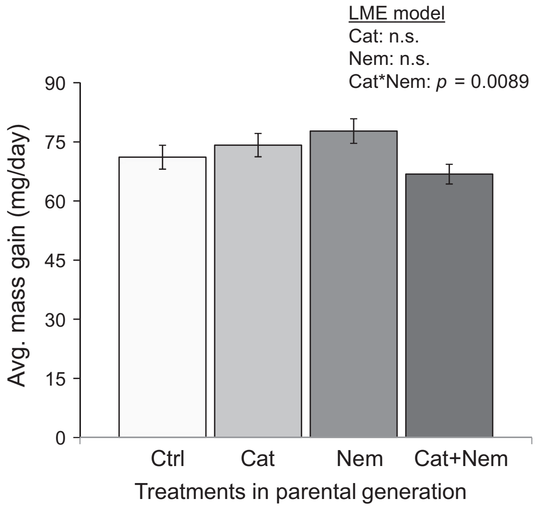

FIGURE 3 Average mass gain per day (mg) of the *Manduca sexta* larvae in the transgenerational experiment (*M* ± *SE*), each replication is the average of three larvae added on a plant as caterpillar treatment, n.s. stands for not significant. Treatments: Ctrl: control, Cat: Caterpillar only, Nem: Nematode only, and Cat + Nem: Caterpillar followed by nematode herbivory with a lag phase of 5 days

such interactions may differ in time and last across a plant generation. With the help of three different but closely linked experiments, we documented the systemic effects of transient above-ground herbivory on plant traits and subsequent below-ground herbivores in the short term, the long term, and across a plant generation. In the short term, transient above-ground herbivory reduced the shoot and root biomass of the plants. The effect on the vegetative biomass disappeared in the long term, while a significant impact on quantitative and qualitative seed traits remained. Transient above-ground herbivory generally had a positive influence on nematode performance. Interestingly, above- and below-ground herbivory in the parental generation increased plant resistance against above-ground herbivores in the progeny plants, while nematode herbivory in the parental generation increased the root biomass of progeny plants, irrespective of herbivore presence. Such transgenerational legacy effects of parental herbivory treatments may suggest priming responses as the changed plant traits are associated with increased plant performance.

4.1 | Short- and long-term effects of transient above-ground herbivory on nematode performance

A meta-analysis of studies on plant-mediated above- and below-ground herbivore interactions (Johnson et al., 2012) showed that above-ground herbivores arriving first on the host plant generally have negative effects on the survival of below-ground herbivores but increase their population growth rate and fecundity. We found contrasting results in our short- and long-term experiments; therefore, we could not confirm the hypothesis of adverse effects of earlier transient above-ground herbivory on subsequent below-ground herbivores. In the short-term experiment, the effect was neutral, while in the long-term experiment, we found generally positive effects of above-ground herbivores. Above-ground herbivory significantly increased the number of galls above 2 mm in size and tended to increase the total number of galls and egg masses of the nematodes. This latter result suggests a long-term legacy effect of the transient above-ground herbivory, which lasted for only 5 days. In a study on plant-mediated linkages between above- and below-ground herbivores in *N. tabacum*, a close relative of *N. attenuata*, Kaplan et al. (2008) also showed that the shoot herbivores *M. sexta* and *Trichoplusia ni* facilitate the performance of nematodes (*M. incognita*) as a result of the reallocation of photoassimilates from shoots to roots in response to feeding damage. In another study, Johnson, Hawes, and Karley (2009) documented that leaf-sucking aphids (*Rhopalosiphum padi*) enhance the growth of root-feeding wireworms (*Agriotes* spp.) in barley *Hordeum vulgare* by increasing the concentration of root minerals, particularly sulphur.

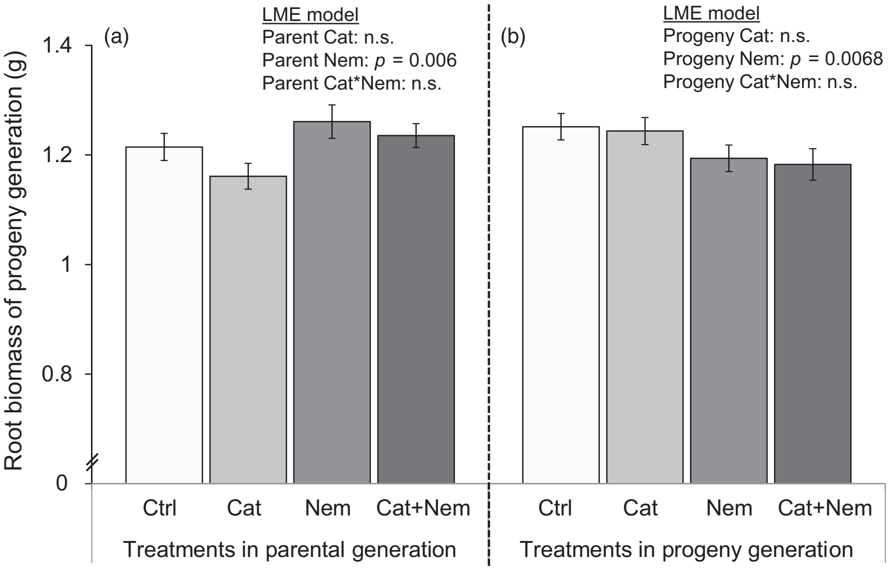

FIGURE 4 Root biomass (g dry mass) of the plants from the transgenerational experiment, based on treatments in parental generation (a) and based on treatments in progeny generation (b) (*M* ± *SE*), n.s. stands for not significant. Treatments: Ctrl: control, Cat: Caterpillar only, Nem: Nematode only, and Cat + Nem: Caterpillar followed by nematode herbivory with a lag phase of 5 days

Antagonistic interactions between above- and below-ground herbivores are often associated with the induction of defensive compounds, whereas facilitation is usually driven by nutrient reallocation. As a tolerance response, plants are known to protect their valuable nutrients, which may later be used for regrowth, by translocating them away from the site of herbivory. In addition, such diversion of nutrients often results in the poor nutritional quality of the feeding site (Babst et al., 2005; Gomez et al., 2012; Kaplan et al., 2008). Eventually, such reallocation of nutrients, for example from shoot to root tissue, may positively affect below-ground herbivores. In the short-term experiment, both above- and below-ground herbivory independently increased the C concentration in the leaves and roots, respectively, while the N concentration in roots was reduced by the nematodes, leading to a higher C/N ratio in the root tissue. In the long-term experiment, we found nematode-derived nutrient accumulation in the roots leading to improved root quality, as indicated by the higher concentration of C and N in the roots. In general, the allocations of C and N in the leaf and root tissues were local responses to the corresponding above- or below-ground herbivory, respectively, and independent of each other in our experiments. Contrastingly, Kaplan et al. (2008) reported that above-ground herbivory by *M. sexta* increased C allocation in the root of *N. tabacum* without altering leaf C, while nematodes had no significant impact on plant C contents. Both above-ground herbivores and nematodes have been found to increase microbial activities in the rhizosphere by increasing root exudation/nutrient leakage. This may enhance nutrient cycling and mineralization, thereby increasing the nutrient availability in the rhizosphere (Bardgett, Wardle, & Yeates, 1998; Tu, Koenning, & Hu, 2003). It is suggested as a potential mechanism for the increase of C and N concentrations in roots due to nematode herbivory (Schöning & Wurst, 2016).

4.2 | Short- and long-term effects of herbivory on plant traits and fitness

Our study shows that both the above- and below-ground herbivory had significant but different effects on the growth and fitness of *N. attenuata*. The effects also depended on the time passed since the herbivory event and/or the developmental stage of the plants. The transient above-ground herbivory by *M. sexta* reduced the shoot and root biomass of plants in the short-term experiment. Similar reductions in the shoot and root biomass of *S. dulcamara* plants by the generalist above-ground herbivore *Scirpus exigua* were found in a previous experiment (Kafle, Krahmer, Naumann, & Wurst, 2014). In the long-term experiment, the negative effect of above-ground herbivory on plant biomass disappeared, while below-ground herbivory by nematodes reduced the shoot biomass without altering the root biomass. The reduced shoot and root biomass due to above- and/or below-ground herbivory may limit photosynthesis, nutrient uptake, and allocation, with potential consequences for the subsequent biotic interaction of the plants. For example, in a recent study, Machado et al. (2013) found that simulated *M. sexta* herbivory (mechanically wounded plants treated with *M. sexta* oral secretions) reduced the content of nonstructural carbohydrates in roots resulting in a reduction in regrowth ability of *N. attenuata* plants.

We measured different quantitative and qualitative traits of the seeds produced by the plants under different herbivory treatments in the long-term experiment, as seed production best represents plant fitness for annual plants like *N. attenuata* (Baldwin, 1998). Both above- and below-ground herbivores had significant negative effects on the production of the total number of seed capsules, suggesting a long-term effect of the transient *M. sexta* herbivory, even 95 days after their removal from the plants. Although the number of capsules was decreased by the transient above-ground herbivory, the total number of seeds per capsule was higher in such plants, which led to a compensation of the yield loss. In contrast, nematodes reduced the total seed yield while increasing the individual seed mass. Baldwin et al. (1998) also reported a reduction in the seed yield of *N. attenuata* because of the trade-off between the costly production of nicotine and seed production when the authors applied methyl jasmonate (MeJA) in root tissue to specifically induce nicotine. Consistently, nematodes induced nicotine in roots and reduced seed yield in our long-term experiment. Directing more nutrient reserves to the seeds could be a tolerance response of the plant to herbivory since maternal effects on seed size have been found to have profound effects on seed germination and seedling vigour (Roach & Wulff, 1987). We also found significant changes in the nutritional status of the seeds. In this sense, there was an interactive effect of above- and below-ground herbivory on the seed C/N ratio, which was higher in those plants that received both herbivores. These results show an overall long-term impact of herbivory on plant fitness with potential impact on growth and development of progeny plants. Individual seed mass and seed nutritional reserves represent a few of the fundamental seed characteristics that are directly linked to the success of the next generation (Limami, Rouillon, Glevarec, Gallais, & Hirel, 2002). Once established, deterring the nematodes that manipulate the root tissue to live and feed may be an ineffective effort of the plant in terms of resources. In this case, it may be an alternative strategy to change seed characteristics so as to improve seed vigour and reproductive success in order to promote the next generation.

4.3 | Transgenerational effects of herbivory on plant and herbivore performance

According to a recently proposed priming model (Hilker et al., 2016; Martinez-Medina et al., 2016), plants that are primed by a biotic or abiotic stress (the so-called priming stress) would have an amplified defence or tolerance response to a subsequent stress (the triggering stress). There are not many studies on transgenerational priming, and the required intensity of the priming stress in the parental generation for such inheritable responses is largely unknown. In the present study, we found significant transgenerational effects of above- and below-ground herbivory in the parental generation on progeny plants that also depended on the intensity of the priming stress. The *M. sexta* caterpillar performance on the progeny plants was reduced due to sequential herbivory experience of their parental plants. It is important to note that the transgenerational priming response resulted only from the sequential above- and below-ground herbivory and not from the single herbivory in the parental generation. This suggests that a certain threshold of biotic stress may be required to elicit a transgenerational response, which was reached in our experiment only by sequential above- and below-ground herbivory. The increased C/N ratio of the seeds due to the sequential above- and below-ground herbivory in the parental generation may have contributed to the enhanced resistance of the progeny plants towards the caterpillars. Provisioning of the seeds with nutrients or altering the profile of defensive compounds in the seeds by the mother plant is considered to be one of the major driving mechanisms of transgenerational induction or priming (Agrawal et al., 1999; Holeski et al., 2012). A similar reduction in the weight gain of *P. rapae* caterpillars was found in the progeny of wild radish plants *R. raphanistrum* whose parents were treated with conspecific caterpillars (Agrawal et al., 1999). The authors suggested that the altered profile of defensive glucosinolates in the seeds of caterpillar-treated plants may have resulted in such a transgenerational induction of defence (referred to as a “greater rapidity of induction of plant defenses” instead of priming, possibly because the term “priming” had not yet been coined).

We also found a transgenerational effect of the root herbivory by nematodes on the biomass of the progeny plants. Nematode herbivory in the parental generation significantly increased the root biomass of progeny plants independent of the herbivory in the progeny generation. Root biomass is considered as a key plant trait associated with plant tolerance because of its significance in resource acquisition (Strauss, Watson, & Allen, 2003); although for some plants, the above-ground biomass is more important for the tolerance response (Carrillo & Siemann, 2016). Therefore, it may be assumed that nematode herbivory experienced by parental plants primed the progeny plants to boost their tolerance ability because more roots are likely to be more tolerant to the same number of nematodes. A bigger root system may also support more nematodes. This result also suggests that the transgenerational effect of herbivory is not only limited to chemical defence. Holeski (2007) found that earlier simulated foliar herbivory on *Mimulus guttatus* plants result in increased trichome density on the leaves within the same generation and across generations. Another study showed that the induced status and N availability in parental *N. attenuata* plants prepare their progeny to adapt to the environmental condition that progeny plants may encounter, with varying effect on their germination rate and fitness (van Dam & Baldwin, 2001).

Independent of the treatments in the parental plants, above-ground herbivory in the progeny generation tended to decrease the shoot biomass without any effect on root biomass. In contrast, below-ground herbivory reduced the root biomass without any effect on shoot biomass. Transient above-ground herbivory in the progeny generation significantly facilitated the growth of the nematodes, as shown by a significantly higher number of galls. Although the experimental duration and procedure were similar in the short-term and transgenerational experiment, the above-ground herbivory-induced responses of the plants varied in these two treatments. One possible reason for this could be the dissimilarity in seed source: seeds from naïve plants were used to grow plants for the short-term experiment, while seeds from the plants treated with above- and/or below-ground herbivores in the long-term experiment were used in the transgenerational experiment. However, there was no significant impact of the herbivore treatments in the parental generation on the nematode performance in the progeny generation.

The results from the long-term and transgenerational experiments provide evidence of a legacy effect of the earlier biotic interaction of the plant with herbivores on subsequent biotic interactions. Plant responses such as induction of defence, compensatory growth, and reallocation of nutrients, priming, and epigenetics are considered major drivers of legacy effects (Wurst & Ohgushi, 2015). The legacy effects found across a plant generation in our experiment may be attributed to transgenerational priming, as we found the increased resistance of progeny plants.

5 | CONCLUSIONS

Plants have evolved the ability to discriminate among different biotic and abiotic stresses in order to optimize resource allocation for growth, defence, and reproduction (Walling, 2000). Our study documents how an ecological model plant species responds with resistance, tolerance, and priming strategies upon above- and below-ground herbivory in different developmental stages. It provides the first evidence of transgenerational legacy effects of above- and/or below-ground herbivory via priming of resistance and tolerance. While there is increasing evidence on molecular mechanisms such as DNA and histone modification, and mobile small RNA to eventuate transgenerational stress response in plants (Chinnusamy & Zhu, 2009; Chitwood & Timmermans, 2010; Rasmann et al., 2012), further research is needed to fully delineate the molecular and epigenetic mechanisms of how the information of the past herbivory is stored in the seeds. The considerable fitness costs of herbivory and altered seed traits, together with evidence of transgenerational priming observed in our experiment, suggest that herbivory in one generation may have significant implications for ecological interactions in the next. Further work on plant-mediated interactions between above- and below-ground herbivores should focus equally on changes in tolerance, resistance, and fitness traits of the plants in order to broaden our understanding of the long-term consequences of above- and below-ground interactions.

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AUTHORS' CONTRIBUTIONS

D.K. and S.W. conceived and designed the experiments. D.K. implemented the experiments, collected, and analysed the data and wrote the manuscript. S.W. advised on data analysis and contributed to manuscript preparation.

DATA ACCESSIBILITY

Data are available at the Dryad Digital Repository https://doi.org/10.5061/dryad.7n89v8r (Kafle & Wurst, 2018).

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SUPPORTING INFORMATION

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