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Aboveground–belowground herbivore interactions: a meta-analysis

Scott N. Johnson,[1,8] Katherine E. Clark,[2,3] Susan E. Hartley,[4] T. Hefin Jones,[5] Scott W. McKenzie,[2,5,6] and Julia Koricheva[7]

[1]*Hawkesbury Institute for the Environment, University of Western Sydney, Locked Bag 1797, Penrith NSW 2751 Australia*
[2]*The James Hutton Institute, Dundee DD2 5DA United Kingdom*
[3]*Department of Biology and Environmental Science, School of Life Sciences, University of Sussex, Falmer, Brighton BN1 9QG United Kingdom*
[4]*Department of Biology, University of York, York YO10 5DD United Kingdom*
[5]*Cardiff School of Biosciences, Cardiff University, Cardiff CF10 3AX United Kingdom*
[6]*Centre for Ecology and Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB United Kingdom*
[7]*School of Biological Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX United Kingdom*

Abstract. Research investigating interactions between aboveground (AG) and belowground (BG) herbivores has been central to characterizing AG–BG linkages in terrestrial ecosystems, with many of these interactions forming the basis of complex food webs spanning the two subsystems. Despite the growing literature on the effects of AG and BG herbivores on each other, underlying patterns have been difficult to identify due to a high degree of context dependency. In this study, we present the first quantitative meta-analysis of AG and BG herbivore interactions. Previous global predictions, specifically that BG herbivores normally promoted AG herbivore performance and AG herbivores normally reduced BG herbivore performance, were not supported. Instead, the meta-analysis identified four factors that determined the outcome of AG–BG interactions. (1) Sequence of herbivore arrival on host plants was important, with BG herbivores promoting AG herbivore performance only when introduced to the plant simultaneously, whereas AG herbivores had negative effects on BG herbivores only when introduced first. (2) AG herbivores negatively affected BG herbivore survival but tended to increase population growth rates. (3) AG herbivores negatively affected BG herbivore performance on annual plants, but not on perennials, and these effects were observed more consistently in laboratory than field studies. (4) The type of herbivore was also important, with BG insect herbivores belonging to the order Diptera (i.e., true flies) having the strongest negative effects on AG herbivores. Coleoptera (i.e., beetles) species were the most widely investigated BG herbivores and had positive impacts on AG Homoptera (e.g., aphids), but negative effects on AG Hymenoptera (e.g., sawflies). The strongest negative outcomes for BG herbivores were seen when the AG herbivore was a Coleoptera species. We found no evidence for publication bias in AG–BG herbivore interaction literature and conclude that several biological and experimental factors are important for predicting the outcome of AG–BG herbivore interactions. The sequence of herbivore arrival on the host plant was among the most influential.

Key words: induced plant defense; induced susceptibility; meta-analysis; plant–herbivore interactions; root herbivores; stress response; systemic signals.

Introduction

Recent decades have seen a growing acknowledgement that many of the aboveground (AG) and belowground (BG) processes operating in terrestrial ecosystems are indirectly linked to each other through plant-mediated mechanisms (Wardle et al. 2004, van der Putten et al. 2009, Bardgett and Wardle 2010). Such plant-mediated linkages between AG and BG organisms can have a wide range of influences on the community dynamics of microbes (Wardle et al. 2005), plants (van Ruijven et al. 2005), and herbivores (Kaplan et al. 2008*a*). In particular, the relationship between spatially separated AG and BG herbivores often forms the basis for more complex food webs spanning AG and BG subsystems (Blossey and Hunt-Joshi 2003, Johnson et al. 2008, van der Putten et al. 2009). Despite the number of studies addressing interactions between AG and BG herbivores, the identification of consistent patterns and generalities has so far proved difficult, perhaps reflecting the wide range of study systems and experimental approaches used (Johnson et al. 2008).

A conceptual model proposed by Masters et al. (1993) suggested that AG herbivores were positively influenced by BG herbivores, whereas BG insects were adversely affected by AG insects. The model hypothesized that the removal of fine roots by insect herbivores resulted in reduced water and nutrient uptake by the host plant (see

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[8] E-mail: Scott.Johnson@uws.edu.au

Plate 1), which consequentially led to elevated amino acids and carbohydrates within the plant foliage (see also Brodbeck and Strong 1987, Huberty and Denno 2004). AG herbivores benefited from the increased nutritional levels within the foliage, resulting in improved performance. In contrast, the model proposed that AG herbivory indirectly reduced root biomass, adversely influencing root-feeding herbivores. While the model provides a concise approach to AG–BG herbivore interactions, its general applicability has been questioned due to its reliance on the limited number of studies available at the time and its emphasis on early successional plants (Blossey and Hunt-Joshi 2003).

Other studies have reported how AG and BG insects can interact by systemically inducing plant defense compounds, which consequentially influence the other herbivore (Bezemer and van Dam 2005, Kaplan et al. 2008*b*). Results from such studies have sometimes had contradictory outcomes to those predicted by Masters et al. (1993). Moreover, the research literature tends to be fragmented and often inconsistent, making it difficult to make generalizations or identify patterns for the outcomes of AG–BG interactions. Given recent advances that incorporate added trophic complexity into AG–BG research (van der Putten et al. 2009), it is particularly timely to exploit our increased knowledge and identify the key patterns that underpin such interactions. For example, recent experimental research suggests that the sequence of arrival on a host plant may affect the outcome of the interaction (Erb et al. 2011), but as yet it remains untested whether this is a general pattern.

This study aims to provide the first quantitative review of this research area by adopting a meta-analysis approach to investigate interactions between AG and BG herbivores via their shared host plant. Previous reviews have so far been entirely qualitative, generalizing trends in AG and BG insect interactions by vote counting (Blossey and Hunt-Joshi 2003, Johnson et al. 2008), which does not take into account the magnitude of the effects and the variation in sample size and statistical power among the studies. Meta-analysis has significant advantages over vote-counting and other qualitative review methods as it enables estimation of the magnitude of the effect across several independent studies as well as the analysis of the various sources of variation (Gurevitch and Hedges 2001). In addition, by taking into account variation in sample size, meta-analysis may allow the identification of trends even when the results of individual studies are not statistically significant. In particular, meta-analysis helps to answer questions in particular research areas where individual studies show conflicting results (Arnqvist and Wooster 1995).

The aim of this meta-analysis was to assess whether general rules proposed in relation to interactions between AG and BG herbivores (for example that proposed by Masters et al. 1993) are supported by the existing experimental evidence and to address four questions that may determine the outcome of AG–BG interactions. These were: (1) Does the sequence that herbivores arrive on the plant matter? (2) Which herbivore performance parameters are most affected, and are these effects consistent? (3) Do the outcomes of interactions differ between plant groups (annual vs. perennial and crop vs. natural) and does it matter whether experiments are conducted in the laboratory or the field? (4) Will different types (e.g., insect orders and nematodes) of herbivore have consistent effects on AG–BG interactions?

Methods

The database

Initially, keyword searches were conducted in the Web of Science (ISI) electronic database (1950–2011) to find studies that investigated the relationships between AG and BG herbivores. The keywords "shoot," "leaf," "root," "aboveground," "belowground," "nematode," and "insect" were used in different combinations to maximize the number of studies captured by the search. Reference lists of the captured studies were examined for further relevant studies. In addition, the database was enlarged by Web of Science searches of studies that cited some of the principal papers within this research area (e.g., Masters et al. 1993, Blossey and Hunt-Joshi 2003). Data reported in postgraduate theses and unpublished data kindly provided by authors were also included in the database, data were obtained by contacting the authors directly. The database consisted of 123 observations derived from 35 studies given in Appendix A (full citations in Appendix C). AG herbivores constituted solely of insects, whereas BG herbivores comprised insects and nematodes. While BG herbivory by mammals has been reported (Johnson and Murray 2008), it has so far not been investigated in relation to AG herbivores.

Studies were required to meet a basic set of criteria to be incorporated into the database. The criteria were designed to ensure that the interaction between AG and BG herbivores was clearly discernible from any other treatments or factors in the study. The criteria were (1) studies had to have two treatments, one where only one herbivore from the pairwise interaction was present on the host plant and one where both insects were present; (2) for studies where measurements of herbivore performance were repeated over time, the final measurements were used to prevent pseudoreplication; (3) studies had to provide sufficient statistical information to allow calculation of effect sizes. This consisted of either sample sizes, means and standard errors/standard deviations for both the control and experimental groups, or test statistics such as the F statistic that could be converted into the effect size metric using the MetaWin statistical calculator (Rosenberg et al. 2000). A high proportion of the data were presented graphically and the imaging software Image J (Abramoff et al. 2004) was used to digitize the figures in order to obtain accurate numerical values.

A range of performance parameters and abundance measures were recorded in the studies to determine the influence of BG herbivores on AG herbivores, and vice versa. Performance parameters included relative growth rate (RGR), survival, fecundity, development time, abundance, mass gain, offspring mass, and longevity.

Meta-analysis

In meta-analysis, the choice of how to calculate effect size is primarily based on the form in which the studies report their findings, although other considerations also influence this decision (Osenberg et al. 1999). For this meta-analysis, Hedges' d (Eq. 1) (Hedges and Olkin 1985) was used as the effect size, as the majority of studies reported means, standard errors and sample sizes:

$$d = \left(\frac{\bar{Y}_e - \bar{Y}_c}{\sqrt{\frac{(N_e - 1)(s_e)^2 + (N_c - 1)(s_c)^2}{N_e + N_c - 2}}} \right) \times \left(1 - \frac{3}{4(N_e + N_c - 2) - 1} \right) \qquad (1)$$

where $\bar{Y}_c$ is the mean herbivore performance on the control group of plants, which for this study represents the treatment with only one herbivore type (AG or BG) present on the host plant and $\bar{Y}_c$ is the mean herbivore performance on the experimental group of plants, which represents the treatment where both AG and BG herbivores are present. The sample size and standard deviation of the control and experimental group is given by N_c and s_c, and N_e and s_e, respectively. Hedges' d is a more robust effect size measurement in comparison to other similar effect sizes when sample size is small (Rosenberg et al. 2000). The MetaWin statistical calculator was used to convert other forms of statistics such as the F statistic into Hedges' d where possible.

The influence of BG herbivores on AG herbivores, or vice versa, was quantified by calculating the effect size for each of the pairwise interactions. A positive effect size indicated that presence of the AG herbivores had a beneficial effect on the performance of BG herbivores and vice versa, similarly negative effect sizes indicated detrimental interactions between the herbivores. Larger effect sizes demonstrate a stronger influence between the two herbivores, with an effect size of 0.2 considered to be small, 0.5 moderate and 0.8 large (Cohen 1988). For development time, the sign of the effect was reversed as an increase in development time between the control and experimental groups indicated a negative effect (i.e., increased development time is a detrimental response).

To obtain mean effect sizes ($d+$) for each category of studies, a mixed-effect model was used, as recommended by Gurevitch and Hedges (1999) for ecological data. This model assumes that the variation between the studies within a group originates from both sampling error and random variation. To test whether effect sizes were significantly different from zero, where zero demonstrates that there is no interaction between the AG and BG herbivores, 95% bias-corrected bootstrap confidence intervals were calculated with 4999 iterations (Adams et al. 1997). The interaction between the herbivores was considered to be statistically significant if the confidence intervals did not encompass zero. All analyses were conducted using MetaWin 2.1. (Rosenberg et al. 2000).

To ascertain how performance parameters of AG and BG herbivores were influenced by one another, effect sizes were calculated for the performance parameters measured in each study. Total heterogeneity (Q_t) and between-group heterogeneity (Q_b) were inspected using a chi square test statistics (Hedges and Olkin 1985) to determine, respectively, whether the observed variance in effect sizes was significantly different from that expected by sampling error alone and whether there were significant differences between the effect sizes for different categories. For question 1, categories were AG or BG first on the plant or simultaneous arrival. For question 2, herbivore response variables were RGR, development time, mass/size gain, fecundity, abundance, population growth, survival, and offspring mass. For question 3, categories were annual vs. perennial, crop vs. natural species, and laboratory vs. field study. Finally, question 4 considered insect order (Coleoptera, Diptera, Lepidoptera, Hymenoptera, and Homoptera) together with "other" (undisclosed in three studies) and Nematoda. With the exception of question 2, which specifically considered differences between performance parameter, these responses were pooled for all other questions.

Publication bias

Publication bias in the literature selected was assessed using the funnel plot technique (Light and Pillemer 1989). Effect sizes for AG and BG interactions were plotted against sample size. To illustrate that there is no publication bias, plots should show symmetry around the mean effect size for each group and no correlation between effect size and sample size should be present. Underreporting of nonsignificant results or weak effects will result in a gap in the funnel and a significant correlation between effect size and sample size. Spearman's rank correlations were calculated between effect sizes and sample sizes for AG and BG insect interactions.

Results

Overall, we found no significant difference between the effects of AG herbivores on BG herbivores and vice versa ($Q_b = 2.245$, df = 1, $P = 0.134$), and neither of the effects differed from zero (AG herbivore affects on BG herbivores, $d+ = -0.140$, 95% CI −0.314–0.021, $N = 46$;

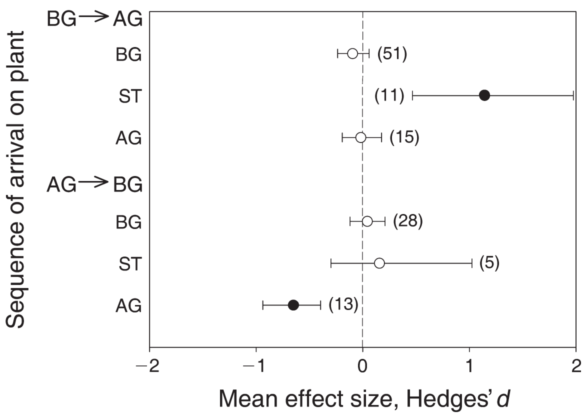

FIG. 1. Influence of sequence of herbivore arrival on a host plant, where ST represents herbivores feeding on the same plant simultaneously, AG is aboveground herbivores, and BG is belowground herbivores. Mean effect size is shown with 95% CI. Effects are considered significant if their associated CIs do not overlap zero (marked by the dashed line). Numbers in parentheses represent the number of studies included in the analysis. Solid circles indicate statistically significant effects.

BG herbivore affects on AG herbivores, $d+ = 0.033$, 95% CI −0.110–0.191, $N = 77$; see Appendix B: Fig. B1). Therefore, the meta-analysis provided no support for directionality of aboveground–belowground herbivore interactions as originally suggested by Masters et al. 1993 (i.e., AG herbivores negatively affected BG herbivores, whereas BG herbivores promoted AG herbivore performance). That said, there were numerous examples of statistically significant interactions reported in the literature, both positive and negative, which effectively neutralized the overall effect in the meta-analysis. Indeed, there was considerable total heterogeneity ($Q_t = 3\ 188.05$, df = 121, $P = <0.001$) suggesting that effects of both AG and BG herbivores varied between studies more than would be expected due to random sampling variation, and we proceeded to examine the causes of this variation.

Sequence of herbivore arrival on the plant

Effects of AG herbivores on BG herbivores depended on the sequence in which herbivores were introduced on their host plant ($Q_b = 17.21$, df = 2, $P < 0.001$). Performance of BG herbivores was significantly reduced only when AG herbivores were introduced on the host plants first, whereas when AG and BG herbivores were introduced simultaneously or BG herbivores were introduced first, BG performance was not significantly affected (Fig. 1). The order of introduction also significantly affected the impacts of BG herbivores on AG herbivores ($Q_b = 25.43$, df = 2, $P < 0.001$); simultaneous introduction of BG and AG herbivores resulted in increased AG performance, but no significant effects were observed when either AG or BG were introduced first (Fig. 1).

Herbivore performance parameter

AG herbivores significantly reduced survival of BG herbivores, but increased their population growth rates and fecundity (Fig. 2; $Q_b = 19.86$, df = 5, $P = 0.001$), whereas effects of BG herbivores on AG herbivores did not depend on the performance parameter measured ($Q_b = 2.288$, df = 5, $P = 0.808$) and none of the AG performance parameters were significantly affected (Fig. 2). It should be noted that while statistically significant, the effects of AG herbivores on BG herbivore fecundity were based on just two studies and this should therefore be treated with caution.

Plant and study type

While the effects of AG herbivores on BG herbivores were generally reported less often, the trends were

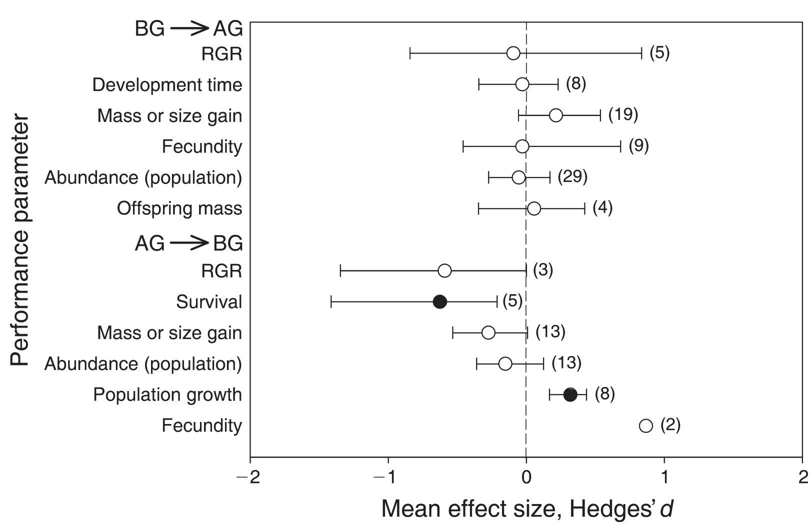

FIG. 2. Influence of different herbivore performance parameters measured on interaction outcomes. Details are as described in Fig. 1. RGR stands for relative growth rate.

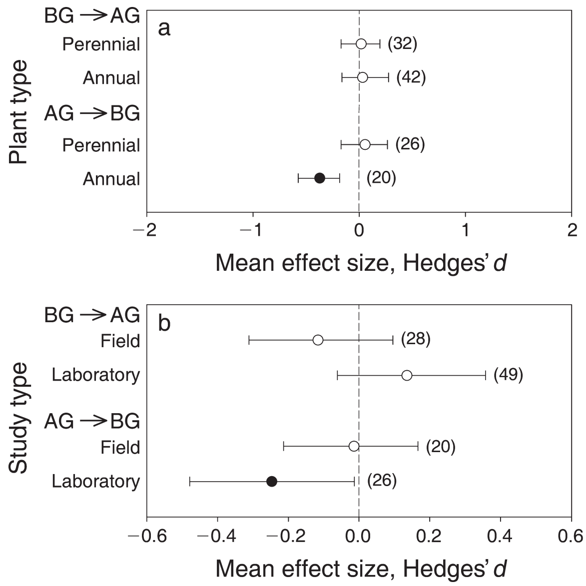

FIG. 3. The effects of (a) plant type (annual or perennial) and (b) study type (laboratory or field) on interaction outcomes. Details as described in Fig. 1.

stronger. The effects of AG herbivores on BG herbivores were significant only on annual plants, but not in studies using perennial species (Fig. 3a; $Q_b = 6.63$, df = 1, $P = 0.010$). In contrast, the effects of BG herbivores on AG herbivores were similar for annual and perennial plants ($Q_b = 0.0117$, df = 1, $P = 0.914$). The outcome of interactions was generally unaffected by whether the mediating plant was a domesticated crop or a natural plant species, either for BG effects on AG herbivores ($Q_b = 0.217$, df = 1, $P = 0.641$) or vice versa ($Q_b = 2.375$, df = 1, $P = 0.123$). Whether the study was conducted in the laboratory or the field also did not generally affect the outcome or magnitude of the AG–BG interaction, either in terms of the impacts of BG herbivores on AG herbivores ($Q_b = 2.689$, df = 1, $P = 0.101$) or vice versa ($Q_b = 2.101$, df = 1, $P = 0.147$; Fig. 3b). A statistically significant negative influence on BG insect herbivores was, however, only detected when experiments were conducted under laboratory conditions (Fig. 3b).

Herbivore type

The effects of BG herbivores on AG herbivores depended on the type of BG herbivore ($Q_b = 10.07$, df = 3, $P = 0.018$) in the interaction (Fig. 4). BG insect herbivores belonging to the insect order Diptera had a negative effect on AG herbivores, whereas considering BG Coleoptera alone (by far the biggest group reported on) demonstrated significant positive impacts on AG Homoptera and negative impacts on AG Hymenoptera (Fig. 4). The difference between BG Coleoptera effects on various AG herbivore groups was only marginally significant ($Q_b = 7.98$, df = 4, $P = 0.092$) at a confidence interval of <90%. It was notable that nematode herbivores did not differ significantly from insect herbivores (Fig. 4). The type of herbivore feeding on the plant AG did not significantly influence performance of BG herbivores overall ($Q_b = 3.41$, df = 3, $P = 0.332$), although only AG Coleoptera and Hymenoptera had significantly negative effects on BG herbivore performance (Fig. 4).

Publication bias

Scatter plots of effect size plotted against sample size of all the data, categorized into AG and BG insect interactions, produced characteristic funnel shapes (funnel plots; see Appendix B: Fig. B2). This indicated that studies with smaller sample sizes showed more

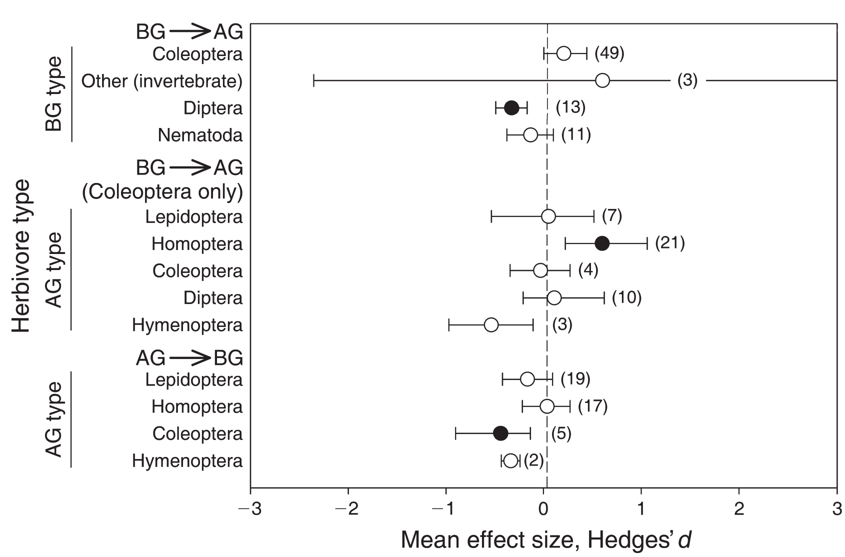

FIG. 4. The influence of herbivore type (insect order or nematode) on interaction outcomes. Details as described in Fig. 1.

variation around the mean effect size than studies with larger sample sizes and there was no obvious correlation between sample size and effect size (BG herbivores affecting AG herbivores, $r_s = -0.13$, $P = 0.264$; AG herbivores affecting BG herbivores, $r_s = 0.05$, $P = 0.756$). These results suggest that there is little publication bias in the meta-analysis.

Discussion

This study has demonstrated that four main factors are important in predicting the outcome of AG–BG herbivore interactions (1) the sequence in which herbivores arrive on a host plant, (2) the herbivore performance parameters being considered, (3) plant life history (annual or perennial) and whether it is being investigated in the laboratory or field, and (4) the type of herbivore involved in the interaction.

Sequence of herbivore arrival on the plant

Recently, Erb et al. (2011) conducted the first study that specifically varied the sequence of arrival of AG herbivores in relation to BG herbivores and demonstrated that negative impacts on BG herbivores only manifested themselves when the AG herbivore arrived first. They posed the question whether this might be a general pattern, but concluded that the lack of empirical evidence made this difficult to answer. Meta-analysis allowed the present study to address this question and demonstrated that the sequence of herbivore arrival on a host plant is crucial in determining the outcome of the interaction. As in the study of Erb et al. (2011), we found that AG herbivores negatively affected BG herbivores when they arrived first, but not when arriving at the same time or after BG herbivores. One possible reason for this is that sustained prior AG herbivory may be needed to induce defenses in the roots systemically or else prime the plant for induction before root herbivory. Alternatively, AG herbivory may alter root location chemical cues (Johnson and Gregory 2006) making the plant less attractive or acceptable to BG herbivores (e.g., Erb et al. 2011).

BG herbivores effects depended on sequence of arrival also, but differently to AG herbivores. BG herbivores typically had positive effects on AG herbivores when they simultaneously shared a host plant, but not when they arrived before or after AG herbivores. This seems consistent with induced susceptibility arising from reduced resistance traits or increases in nutritionally beneficial compounds. The fact that AG herbivores were less affected by prior BG herbivory may arise because the AG herbivores in these studies were unaffected by any induced defenses (e.g., aphids; see discussion in *Herbivore type*) or plants had recovered from root attack and stress-induced increases in foliar nutrients had dissipated. Conversely, earlier arrival of AG herbivores may deter root herbivory (discussed in last paragraph), reducing BG herbivore impacts on plant chemistry or traits that affect AG herbivores.

Plate 1. Red raspberry (*Rubus idaeus*) forms the basis of several aboveground–belowground herbivore interactions. The image is reproduced courtesy of The James Hutton Institute, UK.

Herbivore performance parameter

The meta-analysis showed that choosing which performance parameter to measure in AG–BG herbivore experiments could affect the outcome, and therefore the perceived direction of the interaction. For example, AG herbivores tended to reduce survival but increase population growth rates of BG herbivores. This seems to be contradictory at first, but there is evidence that fewer BG herbivores feeding initially on plants allows compensatory root growth and with reduced competition to begin with, BG herbivores could ultimately become more abundant (e.g., Clark et al. 2012). At the very least, this finding shows the importance of measuring several performance parameters simultaneously in AG–BG experiments to allow accurate assessment of the direction of the interaction.

Plant and study type

AG–BG herbivore interactions were initially studied in short lived, early succession plant species, but negative impacts of AG herbivores on BG herbivores may be much less apparent in longer lived, late succession plant species (Blossey and Hunt-Joshi 2003). The meta-analysis supports this statistically and showed that negative impacts of AG herbivores manifested themselves on annual plants, but not on perennial species. This view has previously been difficult to validate because of the lack of studies on perennial plant species, but this study now provides quantitative support for it. In addition, the existing perception that AG herbivores negatively affect BG herbivores was largely derived from short term lab studies (Blossey and Hunt-Joshi 2003). The meta-analysis showed that the negative effects of AG herbivores on BG herbivores are generally only seen in short-term laboratory studies and not in field studies. Considering that BG herbivores, usually the larval stages of herbivores with AG adult stages, usually have a long lifespan and can become abundant in mature communities, it seems intuitive that they are likely to be better competitors in longer term field conditions (Johnson and Murray 2008). This meta-analysis therefore reiterates the need to validate laboratory observations of AG–BG herbivore interactions with field-based studies (see discussions in Vandegehuchte et al. [2010] and van Dam and Heil [2011]).

Herbivore type

While this study is the first time that this has been demonstrated statistically, there has been ongoing speculation that sap-feeding herbivores (e.g., Homoptera) are the main AG beneficiaries from the plant being attacked by BG herbivores (Johnson et al. 2008). Indeed, this type of root damage is known to gardeners to result in a "weakening" of resistance in the shoots to aphids (van Dam and Heil 2011). Root herbivory may positively affect aphids because it represents a type of discontinuous, or variable, stress (as predicted by the pulsed stress hypothesis proposed by Huberty and Denno [2004]). BG herbivores feed intermittently (Johnson and Murray 2008) so it is conceivable that the plant undergoes bouts of stress and recovery of turgor, which allows aphids to access stress induced increases in leaf nitrogen (Huberty and Denno 2004). As phloem feeders, they may circumvent the effects of any systemically induced defense compounds since these generally occur in low concentrations in the phloem sap (Raven 1983). Other patterns are less easy to explain, such as the tendency for BG Diptera to have negative effects on AG herbivores. This may arise because many of these studies were concerned with *Delia* spp. root flies feeding on brassicas, which are highly inducible in terms of defensive chemistry (Hopkins et al. 2009), and are therefore more likely to have negative effects on AG herbivores. Studies that explore effects with other systems and taxa would inevitably help determine the generality of such findings.

Conclusions

This meta-analysis suggests that the initial global predictions about AG–BG herbivore interactions are generally inapplicable, though it has provided qualitative and statistical support for some previous propositions about AG–BG herbivore interactions. More importantly, the analysis has revealed several novel patterns that may offer some alternative global predictions. In particular, the importance of the sequence arrival of herbivores on a plant, and the fact that this differs for AG and BG herbivores, suggests that mechanisms underpinning AG–BG interactions fundamentally differ depending on the direction and strength of the interaction. The differences in how herbivore performance traits change in relation to AG–BG interactions is also significant, since the choice of performance parameter to be measured could affect the interpretation of the interaction. The field of AG–BG ecology continues to rapidly expand, with researchers attempting to incorporate ever more trophic complexity into experiments and models. In presenting this analysis, we aim to encourage progress in this field by reporting the underlying patterns of AG–BG herbivore interactions, which are so often the cornerstone of more complex AG–BG food webs.

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Literature Cited

Abramoff, M. D., P. J. Magelhaes, and S. J. Ram. 2004. Image processing with Image J. Biophotonics International 11:36–42.

Adams, D. C., J. Gurevitch, and M. S. Rosenberg. 1997. Resampling tests for meta-analysis of ecological data. Ecology 78:1277–1283.

Arnqvist, G., and D. Wooster. 1995. Meta-analysis—synthesizing research findings in ecology and evolution. Trends in Ecology and Evolution 10:236–240.

Bardgett, R. D., and D. A. Wardle. 2010. Aboveground-belowground linkages. Oxford University Press, Oxford, UK.

Bezemer, T. M., and N. M. van Dam. 2005. Linking aboveground and belowground interactions via induced plant defenses. Trends in Ecology and Evolution 20:617–624.

Blossey, B., and T. R. Hunt-Joshi. 2003. Belowground herbivory by insects: influence on plants and aboveground herbivores. Annual Review of Entomology 48:521–547.

Brodbeck, B., and D. Strong. 1987. Amino acid nutrition of herbivorous insects and stress to host plants. Pages 347–364 *in* P. Barbosa and J. C. Schultz, editors. Insect outbreaks: ecological and evolutionary perspectives. Academic Press, New York, New York, USA.

Clark, K. E., S. E. Hartley, R. M. Brennan, K. MacKenzie, and S. N. Johnson. 2012. Investigating preference–performance relationships in aboveground-belowground life cycles: a laboratory and field study with the vine weevil (*Otiorhynchus sulcatus*). Bulletin of Entomological Research 102:63–70.

Cohen, J. 1988. Statistical power analysis for the behavioural sciences. Lawrence Erlbaum Associates, Hillsdale, New Jersey, USA.

Erb, M., C. A. M. Robert, B. E. Hibbard, and T. C. J. Turlings. 2011. Sequence of arrival determines plant-mediated interactions between herbivores. Journal of Ecology 99:7–15.

Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology 80:1142–1149.

Gurevitch, J., and L. V. Hedges. 2001. Meta-analysis: combining the results of independent experiments. Pages 347–369 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Oxford University Press, Oxford, UK.

Hedges, L. V., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, New York, New York, USA.

Hopkins, R. J., N. M. van Dam, and J. J. A. van Loon. 2009. Role of glucosinolates in insect-plant relationships and multitrophic interactions. Annual Review of Entomology 54:57–83.

Huberty, A. F., and R. F. Denno. 2004. Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85:1383–1398.

Johnson, S. N., T. M. Bezemer, and T. H. Jones. 2008. Linking aboveground and belowground herbivory. Pages 153–170 *in* S. N. Johnson and P. J. Murray, editors. Root feeders—an ecosystem perspective. CABI, Wallingford, UK.

Johnson, S. N., and P. J. Gregory. 2006. Chemically-mediated host-plant location and selection by root-feeding insects. Physiological Entomology 31:1–13.

Johnson, S. N., and P. J. Murray, editors. 2008. Root feeders—an ecosystem perspective. CABI, Wallingford, UK.

Kaplan, I., R. Halitschke, A. Kessler, B. J. Rehill, S. Sardanelli, and R. F. Denno. 2008*a*. Physiological integration of roots and shoots in plant defense strategies links above- and belowground herbivory. Ecology Letters 11:841–851.

Kaplan, I., R. Halitschke, A. Kessler, S. Sardanelli, and R. F. Denno. 2008*b*. Constitutive and induced defenses to herbivory in above- and belowground plant tissues. Ecology 89:392–406.

Light, R. J., and D. B. Pillemer. 1989. Summing up: the science of reviewing research. Harvard University Press, Harvard, Massachusetts, USA.

Masters, G. J., V. K. Brown, and A. C. Gange. 1993. Plant mediated interactions between aboveground and belowground insect herbivores. Oikos 66:148–151.

Osenberg, C. W., O. Sarnelle, and D. E. Goldberg. 1999. Meta-analysis in ecology: concepts, statistics, and applications. Ecology 80:1103–1104.

Raven, J. A. 1983. Phytophages of xylem and phloem—a comparison of animal and plant sap-feeders. Advances in Ecological Research 13:135–234.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin—statistical analysis for meta-analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

van Dam, N. M., and M. Heil. 2011. Multitrophic interactions below and above ground: en route to the next level. Journal of Ecology 99:77–88.

Vandegehuchte, M. L., E. de la Peña, and D. Bonte. 2010. Interactions between root and shoot herbivores of *Ammophila arenaria* in the laboratory do not translate into correlated abundances in the field. Oikos 119:1011–1019.

van der Putten, W. H., et al. 2009. Empirical and theoretical challenges in aboveground-belowground ecology. Oecologia 161:1–14.

van Ruijven, J., G. B. De Deyn, C. E. Raaijmakers, F. Berendse, and W. H. Van der Putten. 2005. Interactions between spatially separated herbivores indirectly alter plant diversity. Ecology Letters 8:30–37.

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. Science 304:1629–1633.

Wardle, D. A., W. M. Williamson, G. W. Yeates, and K. I. Bonner. 2005. Trickle-down effects of aboveground trophic cascades on the soil food web. Oikos 111:348–358.

Supplemental Material

Appendix A

List of studies used in the meta-analysis indicating aboveground (AG) and belowground (BG) herbivore, herbivore type, plant species, performance parameter, and which herbivore was affected (*Ecological Archives* E093-208-A1).

Appendix B

Figures containing a histogram of frequency of effect sizes on AG and BG herbivores and a funnel plot of effect size and sample sizes indicating absence of publication bias (*Ecological Archives* E093-208-A2).

Appendix C

Full list of literature citations for studies used in the meta-analysis (*Ecological Archives* E093-208-A3).