PLANT-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Sources of variation in plant responses to belowground insect herbivory: a meta-analysis

Elena L. Zvereva · Mikhail V. Kozlov

Abstract Growing interest in belowground herbivory and the remarkable diversity of the accumulated information on this topic inspired us to quantitatively explore the variation in the outcomes of individual studies. We conducted a meta-analysis of 85 experimental studies reporting the effects of root-feeding insect herbivores (36 species) on plants (75 species). On average, belowground herbivory led to a 36.3% loss of root biomass, which was accompanied by a reduction in aboveground growth (-16.3%), photosynthesis (-11.7%) and reproduction (-15.5%). The effects of root herbivory on aboveground plant characteristics were significant in agricultural and biological control studies, but not in studies of natural systems. Experiments conducted in controlled environments yielded larger effects on plants than field experiments, and infestation experiments resulted in more severe effects than removal studies employing natural levels of herbivory. Simulated root herbivory led to greater aboveground growth reductions than similar root loss imposed by insect feeding. External root chewers caused stronger detrimental effects than sap feeders or root borers; specialist herbivores imposed milder adverse effects on plants than generalists. Woody plants suffered from root herbivory more than herbaceous plants, although root loss was similar in these two groups. Ever-green woody plants responded to root herbivory more strongly than deciduous woody plants, and grasses suffered from root herbivory more than herbs. Environmental factors such as drought, poor nutrient supply, among-plant competition, and aboveground herbivory increased the adverse effects of root damage on plants in an additive manner. In general, plant tolerance to root herbivores is lower than tolerance to defoliating aboveground herbivores.

Keywords Plant growth · Photosynthesis · Reproduction · Root · Tolerance

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Introduction

Plants allocate 50–90% of their biomass to belowground parts (Andersen 1987; Bazzaz et al. 1987; Blossey and Hunt-Joshi 2003). Herbivores feeding on belowground plant parts (roots, rhizomes and storage organs) may substantially reduce the fitness and survival of plants, thus affecting not only the net primary productivity of ecosystems but also the relative abundance of plants, species diversity, and the succession of natural vegetation (Brown and Gange 1990; van der Putten 2003; Stein et al. 2010). Many root herbivores are important agricultural pests, and some species are used as biological control agents (Brown and Gange 1990; Blossey and Hunt-Joshi 2003).

The importance of studying root-feeding herbivores in order to understand the dynamics of plant communities in both natural and managed ecosystems has been underscored in a number of narrative reviews (Andersen 1987; Brown and Gange 1990; Hunter 2001, 2008; Blossey and Hunt-Joshi 2003). A common point of all of these reviews is that herbivore research has largely ignored belowground herbivory. The phrase "out of sight, out of mind" reflects

the previous attitude of many ecologists (except for those studying agricultural pests) to belowground processes (Brown and Gange 1990; Hunter 2001). However, the most recent review (Blossey and Hunt-Joshi 2003) demonstrated considerable growth in the number of publications on root herbivory, especially due to the development of biological control research.

As in the case of aboveground herbivory (Maschinski and Whitham 1989; Wise and Abrahamson 2005), the reported effects of root herbivores on plant performance constitute a continuum from positive to strongly negative (Blossey and Hunt-Joshi 2003). This diversity in responses, which may be related to the experimental methods used, the study system, or environmental characteristics, emphasises the urgent need to identify common trends and differences from the outcomes of individual studies. This task can only be accomplished through a meta-analysis that (in contrast to a narrative review) allows the magnitude and significance of effects to be assessed across studies and the influences of different study characteristics on the outcomes of the research to be estimated statistically (Gurevitch and Hedges 2001). Moreover, meta-analysis reveals both research and publication biases that may considerably influence the conclusions of narrative reviews (Zvereva and Kozlov 2010). While a number of meta-analyses are devoted to plant responses to aboveground herbivory (Bigger and Marvier 1998; Hawkes and Sullivan 2001; Nykänen and Koricheva 2004; Zvereva et al. 2010), our study is the first to quantitatively explore the accumulated information on the impacts of root herbivory on plants by means of a meta-analysis. This numerical assessment is needed, in particular, to incorporate the effects caused by root herbivory into biogeochemical ecosystem models (Wolf et al. 2008).

We restricted our meta-analysis to experimental studies addressing the effects of belowground herbivory on root biomass and/or associated changes in plant performance. Our goal was to evaluate the average magnitudes of the effect of root damage on plant growth, photosynthesis, and reproduction both alone and in combination with various environmental factors, such as drought, soil nutritional quality, among-plant competition and aboveground herbivory, and to reveal sources of variation in plant responses to root herbivory. In particular, we (1) compared the effects of simulated herbivory and insect feeding; (2) compared changes in the below- and aboveground biomasses of damaged plants; and (3) explored variations associated with taxonomic affinity, feeding habits and the level of host plant specialisation of root herbivores, as well as with taxonomic affinity and the life forms of damaged plants. We also investigated how the methodology of the primary studies may have influenced their results and searched for publication bias. Finally, we used the outcomes of earlier meta-

analyses (Bigger and Marvier 1998; Hawkes and Sullivan 2001; Nykänen and Koricheva 2004; Morris et al. 2007; Zvereva et al. 2010) to compare plant responses to root damage with the consequences of damage imposed by aboveground herbivores.

Methods

Data collection

To be included in our meta-analysis, a study had to fit the following criteria:

1. Plant responses to root damage were studied in the experiments (i.e. observational studies and correlative data were excluded)
2. Root damage was imposed by either insect feeding or simulated herbivory (mechanical root damage)
3. Root damage treatment had an appropriate control
4. Plant responses were measured in terms of growth (including biomass per unit area), reproduction or photosynthesis
5. Means, variances and sample sizes were reported for damaged and control plants, were available from the authors, or it was possible to estimate missing variances from test statistics

We searched for publications that met these criteria in the ISI Web of Science database and on the internet using several keywords reflecting the mode of feeding (e.g. "root," "belowground," "herbivore*") or names of the most common root-feeding insects in combination with "plant growth" or "damage" or "photosynthesis," and further examined the reference lists of all of the identified papers. The search was completed on November 15, 2010.

Data selection and response variables

We extracted data on biomass and/or the linear size of the entire plant, above- and belowground parts or individual organs (both vegetative and reproductive); when both fresh and dry mass were reported, dry mass was preferred. We also used vegetative and reproductive biomass production per unit area and the numbers of organs per plant (shoots, leaves/needles, roots, flowers, fruits, seeds). The included characteristics of photosynthesis were both the photosynthetic rate (measured as the net amount of carbon fixed per unit area of a leaf) and the leaf chlorophyll content (both absolute and relative values).

When a study reported several subsequent measurements of plants, we selected the final measurement for the analysis. When more than one level of herbivore infestation or simulated root damage was studied, we selected the effects

caused by the lowest and the highest treatments to explore the dependence of plant responses on the severity of damage. Our estimations of the overall effects and exploration of the effects of methodology on the outcomes of the primary studies included both levels of damage. However, we excluded low-severity treatments when analysing variation related to the characteristics of herbivores and host plants.

We created an additional database for studies in which the effects of root herbivory on plants were explored both alone and in combination with other environmental factors, such as aboveground herbivory (both simulated and natural), among-plant competition (both inter- and intraspecific), soil moisture regime or soil fertility. This database was used to compare the combined effect with the individual effects of root herbivory and other stressors.

As a rule, we extracted the means, variances and sample sizes from publications or obtained these from the authors (one study: Riedell and Rees 1999). For several publications fitting criteria 1–4, we approximated the variances of the control and treatment groups using the reported means, sample sizes and least significant difference values as described by Zvereva et al. (2010).

Classificatory variables

We classified all studies by research domain into the following categories: agricultural and forestry studies (agricultural studies hereafter) dealing with crop plants and plants used in greenery or reforestation in association with their pest species; biological control studies (invasive plants in association with biocontrol agents); or basic ecology studies, usually dealing with natural systems (wild plants in association with their natural herbivores).

The variables related to experimental design included the experimental environment: outdoors (field or common garden) versus controlled (greenhouse, glasshouse, growing chamber, laboratory); the duration of the experiment: single-season versus multiyear; and the method of root damage: mechanical versus insect feeding. Studies manipulating herbivores were divided into two groups: experiments comparing artificially infested plants with uninfested controls (infestation studies hereafter) and those comparing naturally infested plants with plants from which herbivores were removed, usually by an insecticide treatment (removal studies hereafter). We also explored the effects of the intensity of damage by comparing the lowest and highest treatment levels (both mechanical and imposed by insect feeding).

Herbivores were classified according to their high-rank taxonomy (following the Fauna Europaea: http://www.faunaeur.org), feeding habits (external chewers, sap feeders and borers) and level of host plant specialisation. When herbivore specialisation was not mentioned in the case

study, we classified herbivores feeding on plants of a single genus as specialists and herbivores feeding on plants from two or more genera as generalists.

Plants were classified according to their basic life form: herbaceous or woody. Within the woody plants, we contrasted classes (Gymnospermae and Angiospermae) and life forms (deciduous and evergreen); within the herbaceous plants, we compared herbs and grasses, as well as annual and perennial species (species that can be both annual and perennial were excluded from the latter analysis).

Meta-analysis

Hedges's d measure of the effect size (ES) was calculated as the difference between the means of the experimental and control data divided by the pooled standard deviation and weighted by sample size. The mean effect sizes for each treatment were calculated and compared using the Meta-Win 2.0 program (Rosenberg et al. 2000). The treatment was considered to have a statistically significant effect if the 95% confidence interval (CI) of the mean effect size did not include zero (Gurevitch and Hedges 2001). All analyses were performed using random effects categorical models, assuming that the studies differed not only by sampling error but also by a random component of the ESs (Rosenberg et al. 2000). For comparisons between groups of studies, we calculated between-group homogeneity (Q_B) and tested it against the χ^2 distribution with N (the number of groups) minus one degrees of freedom (Gurevitch and Hedges 2001). Publication bias was examined by correlating effect size with sample size (Møller and Jennions 2001).

Additional analyses

The proportion of growth reduction was calculated by averaging the ratio between the means of the experimental and control plants. For a subset of studies that simultaneously measured changes in both below- and aboveground biomass, we regressed the ESs calculated for aboveground parts against the ESs calculated for roots (SAS REG procedure; SAS Institute 2009). The proportions of non-negative effect sizes in the different databases were compared using a Kruskal–Wallis test (SAS NPAR1WAY procedure; SAS Institute 2009).

Results

Databases

The main database used to examine the effects of root herbivory included 453 ESs extracted from 85 papers published between 1941 and 2010 [see Electronic supplementary

material (ESM) 1–2]. These publications reported root losses (57 papers, 147 ESs), as well as changes in growth characteristics of aboveground plant parts (65 papers, 229 ESs) or the whole plant (13 papers, 19 ESs), in various reproductive characteristics (21 papers, 41 ESs) and in measures related to photosynthesis: chlorophyll content (2 papers, 2 ESs) and photosynthetic rate (8 papers, 15 ESs). The production per unit area was measured in three studies for vegetative biomass (6 ESs) and in three studies for seed/fruit yield (6 ESs).

The effects of root herbivory were documented for 75 plant species (33 woody and 42 herbaceous) from 27 families. The amount of data obtained for woody plants was approximately one-third the amount of data for herbaceous plants (22 papers, 107 ESs and 62 papers, 345 ESs, respectively); one study (1 ES) did not discriminate between the roots of different forest plants. The best studied woody plants were citruses (*Citrus* spp.; 29 ESs, or 26.8% of all woody plant data). Among herbaceous species, the largest amount of information (80 ESs, or 23.1% of all herbaceous plant data) was obtained for corn (*Zea mays*).

The effects of insect feeding were explored more frequently than the effects of simulated herbivory (71 and 14 papers, respectively). Root-damaging insects included 36 species from 14 families of 4 orders (Hemiptera, Coleoptera, Lepidoptera, Diptera), among which beetles were investigated most intensively (25 species, 336 ESs). Six studies (11 ESs) considered damage imposed by natural multispecies complexes of root-feeding insects. Most of the studied herbivores were agricultural or forestry pests (20 species, 320 ESs) or weed control agents (8 species, 48 ESs).

The second database (ESM 3), which was created to explore the combined effects of root herbivory and other environmental factors, included 256 ESs extracted from 27 papers that investigated the interactions of root herbivory with aboveground herbivory (12 papers), among-plant competition (5 papers), drought (4 papers) and soil fertilisation (6 papers).

Overall effects of root herbivory

Root herbivory caused significant decreases in all of the investigated plant performance characteristics (Fig. 1). The magnitudes of both the effect on the size of aboveground plant parts (measured as biomass, height, stem diameter, or leaf area) and the effect on the number of plant parts (stems, leaves, fruits, or seeds) (Fig. 1) were similar, allowing us to combine these characteristics in the further analyses.

An observed overall 36.3% loss of root biomass was accompanied by a reduction in aboveground growth by 16.3%, reproductive characteristics by 15.5% and photosynthetic parameters by 11.7%. For studies reporting losses
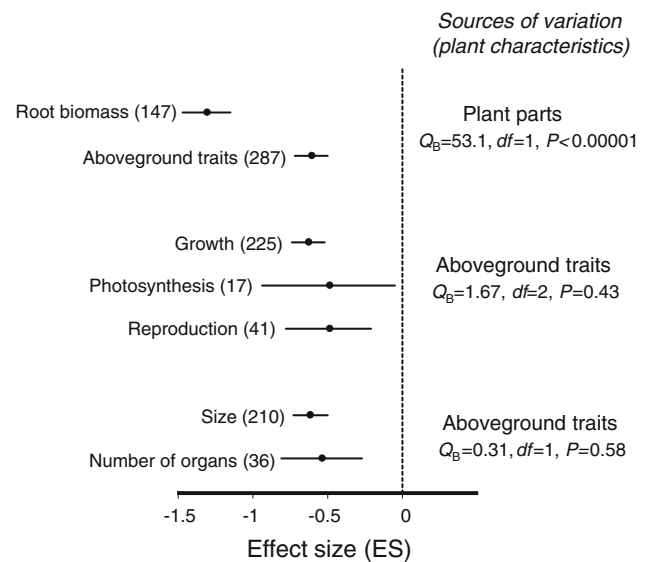

Fig. 1 Overall effects (mean Hedges's d effect sizes) of root herbivory on below- and aboveground plant performance characteristics. *Horizontal lines* denote 95% confidence intervals; sample sizes are shown in *brackets*. The individual effect is significant if the 95% confidence interval does not include zero. Significant ($P < 0.05$) Q_B values indicate between-group heterogeneity

in both below- and aboveground plant biomass, the decrease in aboveground size was proportional to root loss ($d_{above} = -0.389 + 0.213 \times d_{below}$; $R^2 = 0.078$, $F_{1, 102} = 8.60$, $P = 0.0042$).

Variations related to research domain

The agricultural and weed control studies yielded stronger overall adverse effects than basic ecology studies (Fig. 2). This pattern was detected both within infestation experiments ($d = -0.88$, $n = 327$, CI $= -1.98$ to -0.77 and $d = -0.43$, $n = 40$, CI $= -0.70$ to -0.16, respectively; $Q_B = 8.99$, $df = 1$, $P = 0.003$) and within simulation experiments ($d = -1.44$, $n = 33$, CI $= -1.81$ to -1.06 and $d = -0.81$, $n = 30$, CI $= -1.14$ to -0.48, respectively; $Q_B = 6.81$, $df = 1$, $P = 0.009$), indicating that the overall difference (Fig. 2) is not explained by the preferred method of manipulation. Consequently, studies of managed systems reported greater effects than studies of natural systems ($d = -0.99$, $n = 305$, CI $= -1.10$ to -0.88 and $d = -0.58$, $n = 148$, CI $= -0.72$ to -0.44, respectively; $Q_B = 19.8$, $df = 1$, $P = 0.00001$). The decreases in the magnitude of the effect with increase in sample size found in agricultural ($\tau_B = 0.177$, $n = 305$, $P < 0.00001$) and weed control ($\tau_B = 0.208$, $n = 48$, $P = 0.048$) studies suggested that the outcomes of applied studies may have been affected by publication bias. In contrast, the ESs reported in basic ecology studies were independent of sample size ($\tau_B = 0.063$, $n = 100$, $P = 0.35$), indicating an absence of publication bias in this research domain.
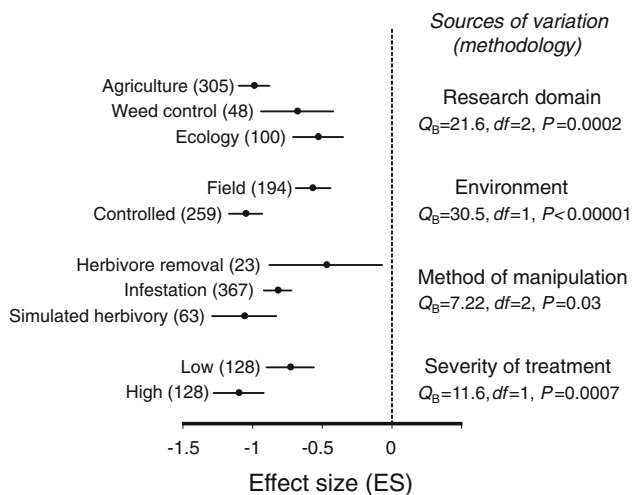
Fig. 2 Effects of methodology on plant responses to root herbivory. For explanations, consult Fig. 1

Variations related to methodology

The method of manipulation influenced the outcomes of the experiments (Fig. 2). Although simulation treatments on average removed a smaller proportion of root biomass than herbivores ($d = -0.91$, $n = 21$, CI $= -1.39$ to -0.42 and $d = -1.45$, $n = 126$, CI $= -1.64$ to -1.25, respectively; $Q_B = 4.48$, $df = 1$, $P = 0.03$), they imposed stronger detrimental effects on the growth of aboveground plant parts than root damage by insects ($d = -1.04$, $n = 37$, CI $= -1.31$ to -0.78 and $d = -0.52$, $n = 250$, CI $= -0.62$ to -0.42, respectively; $Q_B = 13.5$, $df = 1$, $P = 0.0002$).

Root herbivory imposed stronger effects on plants in controlled environments compared to field experiments (Fig. 2), but this difference was observed for aboveground traits only ($Q_B = 4.35$, $df = 1$, $P = 0.04$). Among the included field studies, infestation and removal experiments yielded similar effects ($d = -0.53$, $n = 159$, CI $= -0.65$ to -0.41 and $d = -0.44$, $n = 23$, CI $= -0.78$ to -0.09, respectively; $Q_B = 0.30$, $df = 1$, $P = 0.59$), indicating that weaker effects observed in the field were not due to the application of herbivore removal exclusively in the field studies. Moreover, infestation experiments considered separately resulted in stronger effects in the field than in the controlled environments ($d = -0.55$, $n = 159$, CI $= -0.69$ to -0.41 and $d = -1.06$, $n = 208$, CI $= -1.19$ to -0.92, respectively; $Q_B = 26.9$, $df = 1$, $P < 0.00001$). Removal experiments demonstrated that herbivores occurring naturally in soil imposed significant adverse effects on crop plants in agricultural ecosystems ($d = -1.36$, $n = 7$, CI $= -2.08$ to -0.64), but not in non-crop plant natural ecosystems ($d = -0.09$, $n = 16$, CI $= -0.44$ to 0.27; $Q_B = 14.2$, $df = 1$, $P = 0.0002$). A similar difference was observed for infestation experiments ($Q_B = 8.69$, $df = 1$, $P = 0.003$), although

the effects were significant in both agricultural and natural systems ($d = -0.91$, $n = 272$, CI $= -1.03$ to -0.80 and $d = -0.59$, $n = 95$, CI $= -0.77$ to -0.40, respectively).

In studies reporting several levels of simulated damage or infestation rates, the highest damage levels caused larger effects than the lowest damage levels. However, the lowest damage levels still resulted in a significant decrease in plant performance (Fig. 2) in the experiments using both simulated herbivory ($d = -1.03$, $n = 16$, CI $= -1.51$ to -0.55) and infestation treatments ($d = -0.64$, $n = 112$, CI $= -0.81$ to -0.48).

Multiyear experiments with woody plants yielded smaller effects than single-season experiments ($d = -0.04$, $n = 10$, CI $= -0.67$ to -0.60 and $d = -1.30$, $n = 86$, CI $= -1.51$ to -1.09 respectively; $Q_B = 17.5$, $df = 1$, $P = 0.00003$). In contrast, long-term studies with perennial herbaceous plants yielded stronger adverse effects than short-term studies ($d = -1.38$, $n = 11$, CI $= -1.95$ to -0.81 and $d = -0.74$, $n = 109$, CI $= -0.92$ to -0.57, respectively; $Q_B = 5.49$, $df = 1$, $P = 0.02$).

Variations related to herbivore taxonomy and life history

Root-feeding species differed in their impacts on plants ($Q_B = 130.3$, $df = 31$, $P < 0.00001$). This variation was not explained by high-rank taxonomic affinities: differences between the four investigated insect orders were not significant (Fig. 3a). However, we found significant differences between families within the beetles (Coleoptera): the strongest adverse effects on plants were imposed by Curculionidae and Scarabaeidae, whereas the effects of Elateridae and Cerambycidae species were not significant (Fig. 3a). The two most damaging families, Curculionidae and Scarabeidae, did not differ in their effects on plants ($Q_B = 0.21$, $df = 1$, $P = 0.65$). Among species considered in more than two papers, the largest effects on plants were imposed by *Diaprepes abbreviatus* (Coleoptera: Curculionidae) and *Agapeta zoegana* (Lepidoptera: Tortricidae) (Fig. 3a).

Insect feeding guilds differed in their effects on plant performance: external chewers caused detrimental effects that were twice as strong as those caused by sap feeders or borers (Fig. 3b). However, this difference was mostly due to effects on root biomass, while the effects on aboveground parts were similar ($Q_B = 0.44$, $df = 2$, $P = 0.80$). The stronger overall effect of generalist herbivores (Fig. 3b) was due to the removal of a significantly larger portion of the root biomass relative to specialised herbivores ($Q_B = 10.6$, $df = 1$, $P = 0.001$), while the effects of both groups on aboveground plant parts were similar ($Q_B = 0.85$, $df = 1$, $P = 0.36$). This difference in root damage between generalists and specialists was not due to variation between feeding guilds, because within a guild of external chewers,
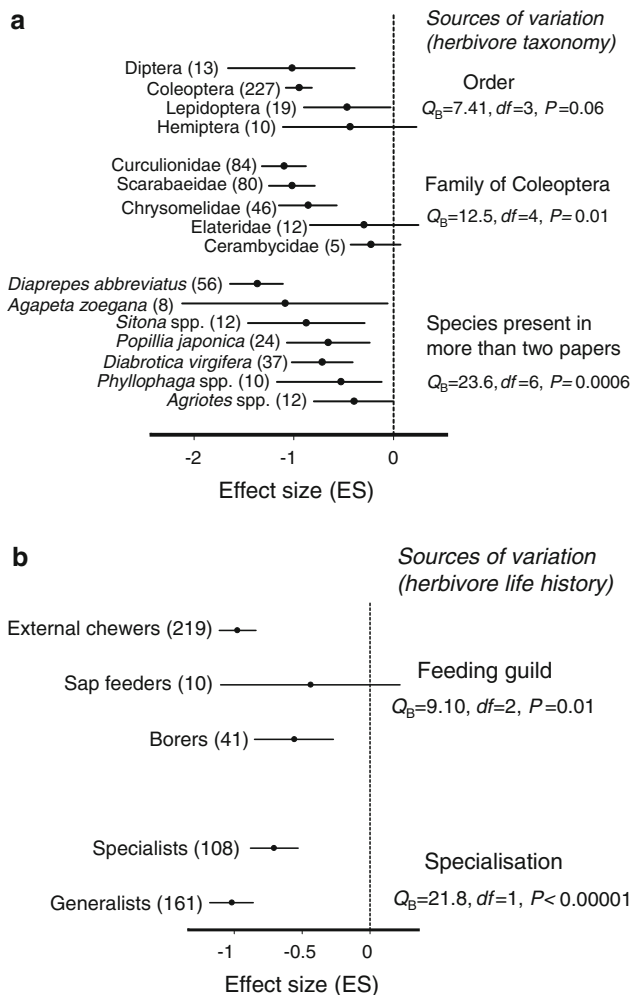
Fig. 3 Effects of insect taxonomic characteristics (**a**) and feeding guild and host plant specialisation (**b**) on plant responses to root herbivory. For explanations, consult Fig. 1

Fig. 4 Effects of plant characteristics on plant responses to root herbivory. For explanations, consult Fig. 1

from root herbivory more than mature individuals ($Q_B = 5.07$, $df = 1$, $P = 0.02$), while we found no difference in the responses among ontogenetic stages for evergreen woody plants ($Q_B = 1.40$, $df = 1$, $P = 0.24$).

Within herbaceous plants, monocots (grasses) suffered from root herbivory more than dicots (herbs), and perennials did not differ from annuals in their responses to root damage (Fig. 4).

The detected patterns were not affected by inevitable differences between herbivores associated with specific groups of plants, as demonstrated by the analyses restricted to a specific group of herbivores (results not shown).

Interactions with environmental factors

The effects of root herbivory on plants were of the same magnitude on average as the effects of aboveground herbivory, competition, drought and nutrient stress ($P = 0.27$–0.76). However, root damage resulted in adverse effects that were twice as strong, on average (Fig. 5), when it was combined with aboveground herbivory ($Q_B = 7.17$, $df = 1$, $P = 0.007$), increased competition ($Q_B = 6.60$, $df = 1$, $P = 0.06$), drought ($Q_B = 6.34$, $df = 1$, $P = 0.01$), or low nutrient supply ($Q_B = 9.67$, $df = 1$, $P = 0.002$).

Discussion

Trends in root herbivory research: plant perspective

The number of studies reporting quantitative estimates of the effects of root herbivory on plants increased rapidly in

generalists still caused greater root losses than specialists ($Q_B = 16.4$, $df = 1$, $P = 0.00005$).

Variations related to plant taxonomy and life form

Woody plants suffered from root herbivory more than herbaceous plants (Fig. 4), although the average root losses were similar in these two groups ($Q_B = 2.28$, $df = 1$, $P = 0.13$). This difference was mostly due to the effects on aboveground growth ($Q_B = 7.06$, $df = 1$, $P = 0.008$), whereas the effects of root herbivory on reproduction did not differ between woody and herbaceous plants ($Q_B = 0.002$, $df = 1$, $P = 0.96$). Within woody plants, gymnosperms did not differ from angiosperms ($Q_B = 0.45$, $df = 1$, $P = 0.51$), but evergreens responded to root herbivory more strongly than deciduous plants (Fig. 4). The latter difference resulted mostly from large effects reported for evergreen leaf-bearing plants (primarily *Citrus* species). Among deciduous woody plants, juveniles suffered
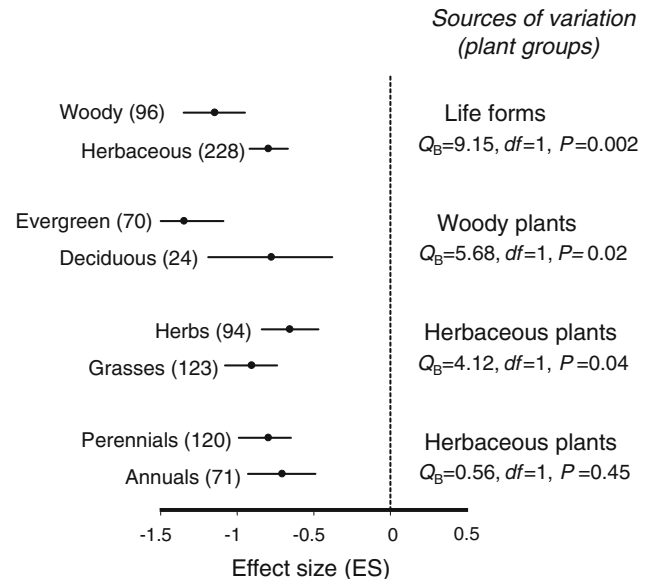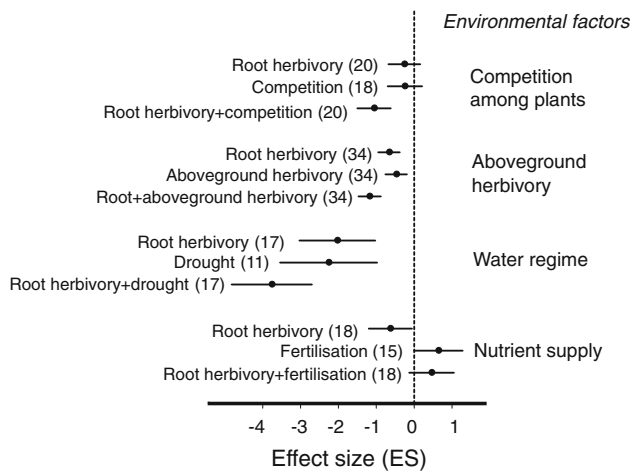
Fig. 5 Individual and combined effects of root herbivory and environmental factors on plant performance. For explanations, consult Fig. 1; for significance of pairwise comparisons, consult text

the early 1990s: 83% of the studies included in our meta-analysis were published from 1991 to 2010. However, our analysis supports the opinion of Blossey and Hunt-Joshi (2003) that the number of publications addressing root herbivores in recent years is growing very slowly: our database includes 36 studies published from 2001 to 2010, which is nearly equal to the 35 studies published from 1991 to 2000. Moreover, Blossey and Hunt-Joshi (2003) estimated that only approximately 10% of root herbivory studies have been conducted in the research domain of basic ecology, and our meta-analysis demonstrated no increase in the interest of basic ecologists on the effects of root herbivory on plant performance (15 studies were published from 1991 to 2000 and 15 from 2001 to 2010). Thus, the amount of "basic" root herbivory research addressing changes in plant growth and productivity is increasing much more slowly than was expected two decades ago (Brown and Gange 1990). This may be at least partly related to considerable difficulties involved in the manipulation and observation of belowground objects. However, the number of studies exploring root feeders as potential biological control agents is growing continuously, and root herbivores are increasingly being used to control invasive plant species (Blossey and Hunt-Joshi 2003). Another rapidly developing research field addresses interactions between above- and belowground herbivores (van Dam and Heil 2011).

General patterns and underlying mechanisms

Our results confirm the conclusion of numerous studies (reviewed by Andersen 1987; Brown and Gange 1990; Hunter 2001, 2008; Blossey and Hunt-Joshi 2003) that belowground damage causes considerable detrimental effects on aboveground plant traits, and our estimate of the

magnitude of this effect (Fig. 1) is similar to the estimate by Morris et al. (2007) (root feeders: $d = -0.55$, CI $= -0.99 \ldots -0.10$, $n = 10$). Detrimental effects result from several processes: (i) decreases in water and nutrition uptake due to direct reductions in root biomass (mostly when fine roots are consumed), or disruption of water and nutrient flows (mostly when the main root is damaged); (ii) consumption of resources stored belowground; (iii) decreases in photosynthetic rates due to water deficits imposed by root damage; (iv) translocation of assimilates to roots for root regrowth; and (v) direct costs of inducible defences (for more details, consult ESM 4).

The processes described above lead to the limitation of all types of resources, and therefore the effects of root herbivory may be very severe, leading not only to growth retardation but even to plant death (Gange et al. 1991; Maron 2001). In agreement with this conclusion, a number of studies found that the detrimental impacts of root herbivory on plants may exceed the effects of aboveground herbivores (Brown and Gange 1989; Maron 1998), although the opposite pattern has been also reported (e.g. Houle and Simard 1996). The magnitude of the aboveground growth responses of woody plants to root herbivory estimated in our meta-analysis ($d = -0.98$) is very similar to the effects caused by defoliators ($d = -1.00$: Nykänen and Koricheva 2004) and sap feeders ($d = -1.06$: Zvereva et al. 2010). Moreover, in both the meta-analysis by Morris et al. (2007) and our meta-analysis of studies addressing the combined effects of above- and belowground herbivory on plants (Fig. 5), the magnitudes of the effects did not differ between above- and belowground herbivores acting alone. Thus, our results do not seem to support the opinion (Ingham and Detling 1986; Brown and Gange 1990; Móron-Ríos et al. 1997) that root herbivores impose generally stronger impacts on plant fitness than aboveground herbivores.

However, although the overall reduction in plant fitness found in three meta-analyses mentioned above was of approximately same magnitude, the mechanisms underlying the impacts of belowground herbivores on plants differ considerably from those of their aboveground counterparts. The proportion of non-negative effect sizes (i.e., those indicating exact compensation or overcompensation) in response to defoliation found in the meta-analysis by Hawkes and Sullivan (2001) was twice as high as the proportion found in response to root herbivory (34.6 and 17.2%, respectively; $\chi^2 = 13.0$, $df = 1$, $P = 0.0003$). Furthermore, while the meta-analysis by Nykänen and Koricheva (2004) demonstrated that defoliation generally causes an increase in photosynthesis, we found that root damage leads to a significant reduction of photosynthesis (Fig. 1). The responses of plants to root feeders are more similar to plant responses to sap feeders (Zvereva et al. 2010), which induce compensatory growth even less frequently than root feeders (8.1

and 17.2%, respectively; $\chi^2 = 15.9$, $df = 1$, $P < 0.0001$). We suggest that this similarity is explained by a reduction of photosynthesis in response to both root feeders (Fig. 1) and aboveground sap feeders (Zvereva et al. 2010). Although the suppression of photosynthesis is underpinned by different mechanisms (discussed for sap feeders by Zvereva et al. 2010), it hampers the compensatory growth of plants in both cases. Moreover, while aboveground herbivory induces defences mostly in leaves, root damage elicits equally strong responses in both leaves and roots (Kaplan et al. 2008), which may result in higher fitness costs.

Notably, in our meta-analysis, only 7% of the ESs calculated for root biomass were non-negative, indicating that the accelerated root growth frequently observed in response to belowground herbivory (Andersen 1987; Brown and Gange 1990) is generally insufficient to compensate for root losses. However, it is possible that this rarity of compensation is explained by measuring plants immediately after the termination of herbivore feeding, whereas most intensive root regrowth may occur later. This hypothesis is supported by the observation of a steady recovery of CO_2 assimilation rates in plants that have been monitored after the termination of root damage (Riedell and Rees 1999).

Interactions with environmental factors

As concluded above, root herbivory imposes strong resource limitations on plants, so the effects of root herbivory on plant performance should be more severe in conditions of low resource availability (Wise and Abrahamson 2005). Our meta-analysis confirmed this prediction: the effects of root herbivory interact with those of drought and nutritional stress, among-plant competition and aboveground herbivory in an additive manner, such that the combined effects considerably (by more than a factor of two) exceed the detrimental effects of both root herbivory alone and the individual effects of other stressors. Consequently, increased supplies of water and nutrients mitigate the adverse impacts of root herbivores on plant growth (Fig. 5; Ladd and Buriff 1979; Gange and Brown 1989). Plants growing at high densities can be water and nutrient stressed (Tilman 1989; Maron 2001), and can experience light limitations (Agrawal 2004). Therefore the additive effects of among-plant competition may be based on the same mechanisms as the effects of drought and nutritional stress. Moreover, plant defences can be compromised when individuals grow at a high density (Karban et al. 1989).

The discovery of a synergy between the effects of above- and belowground herbivory on plant performance is not surprising, because simultaneous damage of different plant parts imposes severe limitations on all of the resources required for plant growth and reproduction. However, the effects of spatially separated herbivores on a common host

plant may be modified by the impacts of these two groups of herbivores on each other. Root herbivores may favour the development of aboveground herbivores by increasing the nutritional value of foliage (Masters et al. 1993; Johnson et al. 2009); in turn, aboveground herbivory may enhance the development of root herbivores (Seastedt et al. 1988; Johnson et al. 2009). These positive interactions may increase herbivore pressure on plants, and the cumulative impact of herbivores attacking different plant tissues is sometimes used to accelerate and improve biological weed control (McEvoy et al. 1991; Malecki et al. 1993). However, the interactions between below- and aboveground herbivory, which recently attracted considerable attention from researchers (reviewed by van Dam and Heil 2011), are complex and variable, so their consequences for plants are context specific.

Study systems and research domains

Our meta-analysis found no effects of root herbivory on plant performance in natural ecosystems. This result is in line with the opinion that at low densities, the effects of root herbivores on plants can be considered neutral (Blossey and Hunt-Joshi 2003 and references therein). Therefore, significance of adverse effects caused by low herbivore densities suggests that in most infestation experiments (85% of which are agricultural studies), the lowest of densities applied still exceed the levels of root herbivory in natural (i.e. unmanaged) ecosystems.

Applied (agricultural and biological control) studies reported significantly stronger reductions in plant growth and reproduction than basic ecology studies. This can be explained by several factors. First, applied studies are goal oriented (as defined by Blossey and Hunt-Joshi 2003), and therefore the selection of study objects is limited to the most damaging species, which are either agricultural pests or biocontrol agents. Second, in applied studies, researchers tend to use extremely high infestation rates that far exceed the herbivory levels in natural systems. This conclusion is supported by the significantly lower effects detected in removal studies, which employ natural levels of herbivory (Fig. 2). Importantly, the same difference between infestation and removal studies was found in meta-analyses of the effects of aboveground herbivory on plants (Bigger and Marvier 1998; Zvereva et al. 2010). Third, the significant publication bias found in applied studies suggests that researchers working in this domain are less likely to publish studies yielding nonsignificant or unexpected effects than researchers working on basic ecological problems. In weed control studies, in particular, the failure to find the desired effect of a potential biocontrol agent may well justify the abandonment of the results. Thus, due to an overrepresentation of applied studies in our database (over 80% of the

ESs), the average negative effect of root herbivory on plant performance is likely to be considerably overestimated. However, overestimation of the magnitude of the effect does not question the suitability of these studies for the exploration of mechanisms or sources of variation in plant responses to root herbivory.

Variations related to methodology

Studies conducted in controlled environments (glasshouse, climatic chamber or the laboratory, with plants being grown in pots or in hydroponics) yield effects twice as strong as the effects seen in field studies. This difference between field and greenhouse studies was also found in a meta-analysis of the effects of sap-feeding herbivores on plant growth (Zvereva et al. 2010). More generally, laboratory studies, by eliminating a substantial portion of natural variability, are likely to produce biased (usually exaggerated) results (discussed by Kozlov et al. 2009). Because plant responses to herbivory are affected by numerous abiotic and biotic factors (Strauss and Agrawal 1999), the lack of these multiple interactions in greenhouse experiments could have contributed to the observed differences. Thus, although studies in controlled environments are vital for exploring the mechanisms behind observed phenomena, the magnitudes of the effects detected in these experiments cannot be directly extrapolated to field conditions.

We have found that the detrimental effects of simulated herbivory on aboveground traits are twice as strong as the effects of natural herbivory (Fig. 2). Our meta-analysis indicates that this difference is not due to stronger root damage in simulation treatments. However, it may be partly explained by different spatial and temporal patterns of root damage (Andersen 1987): while simulated herbivory usually removes a certain proportion of roots all at once, damage by insects accumulates gradually and is partially counterbalanced by root regrowth. Furthermore, many wound-induced defensive responses are elicited by compounds present in insect oral secretions, but do not develop following mechanical tissue damage (Koo and Howe 2009; Poveda et al. 2010). Thus, our results confirm the conclusions of Andersen (1987) and Blossey and Hunt-Joshi (2003) that artificial damage does not mimic damage caused by herbivores.

We conclude that most of the experimental studies addressing the effects of root herbivory on plants apply a methodology (e.g. mechanical root damage, high infestation rates, controlled environments) that unavoidably leads to a considerable overestimation of the effects relative to those observed under natural levels of herbivory. Therefore, results of such experiments should only very cautiously be used to estimate biomass losses due to root herbivory in either natural or managed systems. The most realistic information can be obtained from field studies.

Variations related to herbivores

We discovered two sources of variation related to herbivore feeding habits. First, external chewers impose stronger effects on plants than sap feeders and root borers because they cause greater losses of root biomass. External chewers feed on fine roots, which are the most vulnerable and least defended roots (van Dam 2009), and at the same time, they are most critical for water and nutrient uptake (Eissenstat and Yanai 1997). In contrast, root borers feeding within the main root not only consume resources stored belowground, but they may also disrupt vascular connections between roots and aboveground plant parts. Thus, although insects from different feeding guilds affect plants through different mechanisms and remove a different proportion of the root biomass on average, they cause similar impacts on aboveground plant parts.

Second, unspecialised (generalist) species impose considerably greater detrimental effects on plants than specialised herbivores. This finding supports the conclusions of a meta-analysis of plant responses to sap-feeding aboveground herbivores (Zvereva et al. 2010). The concordance between these two ecologically different groups of herbivores indicates that weaker plant responses to specialised herbivores may appear to be a general phenomenon. The evolution of co-adaptations of herbivores with their hosts is likely to depend on the intimacy of the relationships between them, which is closer for specialist than for generalist feeders. Because some studies have demonstrated the existence of a trade-off between the evolution of plant defences against generalist and specialist herbivores (Johnson et al. 2009), our findings may indicate that specialised root feeders impose stronger selective pressure on host plants during their coevolutionary history than generalists. As a result, plants become adapted to tolerate damage by highly specialised pests better than damage by generalist herbivores.

The stronger adverse effects of generalists cannot be explained by the predominance of external chewers in this group, as among external chewers, the difference between generalists and specialists was also significant. However, this difference may result from the greater root losses caused by generalists. This, in turn, may be related to the large size of scarab beetles, which are the most numerous group of generalist external chewers. More generally, we believe that the differences between the effects on plant performance caused by different insect taxa (Fig. 3a) are explained by their life histories rather than a taxonomic affinity per se.

Variations related to plants

Our meta-analysis revealed the higher sensitivity of woody plants to root herbivory (Fig. 4). This pattern contrasts with the results of Hawkes and Sullivan (2001), who did not find any differences in growth responses to aboveground herbivory between woody plants and herbs. Moreover, based on comparisons of the degree of physiological integration among modules, life span and biomass partitioning among plant organs, Haukioja and Koricheva (2000) argued that woody plants should be more tolerant to herbivory than herbaceous plants. Therefore, we suggest that our result (Fig. 4) was influenced by the predominance of juveniles in studied woody plants (83%), whereas herbaceous plants used in the experiments were generally mature (i.e. had reached reproductive age). Mature plants tolerate herbivory better than juvenile plants (Strauss and Agrawal 1999; Nykänen and Koricheva 2004; Zvereva et al. 2010, but see Barton and Koricheva 2010) because of limitations on resource acquisition and stored reserves in younger plants, and this appears to also be true (at least in deciduous plants) in response to root herbivores, which further hamper resource uptake. The dependence of the effects of root herbivory on plant ontogenetic stage explains a seemingly paradoxical result: the smaller negative effects discovered in long-term studies of woody plants compared to short-term studies. We suggest that this pattern may result from increasing tolerance to herbivory as seedlings grow.

Our meta-analysis demonstrated that the growth of evergreen plants is reduced by root herbivory more than the growth of deciduous plants, and a similar pattern was found in a meta-analysis of woody plant responses to aboveground herbivory (Nykänen and Koricheva 2004). The difference between evergreen and deciduous woody plants may be associated with patterns of biomass allocation: the storage of a larger proportion of biomass in woody tissues allows deciduous species to recover from herbivore damage by mobilising stored energy for compensatory growth (Chapin et al. 1990; Strauss and Agrawal 1999).

Grasses suffer from both below- and aboveground herbivory more than herbs (Fig. 4; Hawkes and Sullivan 2001), which is in agreement with the results of Stein et al. (2010), who found that in natural grassland communities, grasses became more dominant when belowground herbivores were excluded by insecticide treatment. The stronger adverse effects of aboveground herbivory on grasses are usually attributed to different meristem locations, which are apical for herbs and basal for grasses (Haukioja and Koricheva 2000; Hawkes and Sullivan 2001), but this difference cannot explain the greater sensitivity of grasses to belowground herbivory. Stein et al. (2010) suggested that the higher susceptibility of grasses to belowground herbivory results from their more extensive root system, which is

therefore more exposed to root herbivores. However, this explanation is not valid for the majority of experiments included in our meta-analysis, because they were usually established with monocultures.

Additionally, Haukioja and Koricheva (2000) emphasised the fact that woody plants and grasses share a number of life history traits, which may determine similarities in their responses to herbivory. Consistent with this prediction, we found that grasses are more similar to woody plants than to herbs in the magnitude of their response to belowground herbivory (Fig. 4). However, because very little is known about the mechanisms of plant tolerance to root herbivory (Hunter 2001), it seems premature to attempt to identify life history traits responsible for this similarity.

Data gaps, biases and research needs

Our meta-analysis allows reconsidering some data gaps and research needs pointed out in earlier reviews (Andersen 1987; Brown and Gange 1990; Hunter 2001, 2008; Blossey and Hunt-Joshi 2003). Unfortunately, not all of the publications describing the effects of root feeding on plants contained numerical information sufficient to calculate the effect size. In particular, this concerns studies reporting the effects of root herbivory on plant survival: we had to exclude this parameter from the meta-analysis because all of the identified studies (except for one: Maron 2001) contained mean values without measures of variance, and only a few studies reported numbers of dead and surviving plants (which are needed to perform meta-analysis based on odds ratios). Furthermore, many authors tend to present only the results of statistical tests, often omitting the primary data. The relatively scant reporting of summary statistics in recent publications is especially disappointing. Because this problem has been independently discovered in different fields of ecology, we strongly support the suggestion by Paillet et al. (2010) that scientific journals should ask for mean values to always be presented along with their corresponding variances and sample sizes.

Another discovered problem is reporting bias, which affects meta-analyses much more strongly than narrative reviews. Three of the studies included in our database (Saner and Müller-Schärer 1994; Maron 2001; Wurst and van der Putten 2007) presented (on graphs or in tables) only those results that allowed the null hypothesis to be rejected, while no quantitative data were provided for experiments yielding nonsignificant results. This selective reporting may result in an overestimation of the consequences of root feeding on plant performance.

The majority of studies included in our meta-analysis were conducted under controlled conditions. The striking difference observed in the outcomes of "indoor" and "outdoor" experiments (Fig. 2) highlights the need to place

greater emphasis on studying the effects of root herbivory on plants growing in their natural environments. This especially concerns nonagricultural plants, particularly mature trees, for which responses to root herbivory remain virtually unknown. Furthermore, the study design should allow the exploration of compensatory root regrowth after the termination of herbivore feeding.

One of the research shortfalls that became obvious during the course of our meta-analysis is the need to explore plant responses to "normal" levels of root herbivory in natural systems. As we concluded in a meta-analysis of the effects of pollution on insects (Zvereva and Kozlov 2010), field studies on herbivory are more likely to be conducted in sites where herbivore damage is apparent. Therefore, the levels of plant damage calculated from published data are expected to more frequently be attributed to exceptionally high population densities of root herbivores (i.e. outbreaks), rather than to background ("normal") herbivory. Long-term studies of the population dynamics of root feeders in natural ecosystems are needed to compare the consequences of outbreaks with the background damage imposed by herbivores at low population densities.

Finally, the synergy found between the effects of root herbivory and several biotic (competition, aboveground herbivory) and abiotic (water and nutrient availability) factors highlights the urgent need to explore the interactive effects of root herbivory and the primary drivers of global change (temperature, ambient CO_2 and UV-B radiation) on plant performance. Accounting for the sources of variation in the outcomes of primary studies uncovered by the present and earlier meta-analyses (Zvereva and Kozlov 2006; Zvereva et al. 2010) would allow these experiments to be designed in such a way that the obtained information can serve as the basis for realistic predictions of plant performance under future climate conditions.

Conclusions

Our meta-analysis of the effects of belowground herbivory on root losses and associated changes in plant performance revealed significant heterogeneity in the outcomes of experimental studies and identified numerous sources of this variation. Various environmental factors, such as drought, poor nutritional quality of the soil, among-plant competition and aboveground herbivory, increase the adverse effects of root damage on plants in an additive manner. The changes in aboveground plant characteristics are proportional to root losses. The magnitude of the effect on root biomass depends on the feeding habits of herbivores: external chewers cause losses that are twice as great as those due to sap feeders or root borers; changes in aboveground plant characteristics do not depend on insect feeding guilds. Generalists impose

greater adverse effects than specialists, presumably because plants are better adapted to tolerate damage by their specialist consumers. The analysis of compensatory responses suggested that plant tolerance to root herbivores is lower than their tolerance to defoliating aboveground herbivores.

A substantial portion of the variation in the outcomes of primary studies is related to methodological issues (field or controlled environments, simulated or natural herbivory, infestation or removal experiments, the herbivore density applied in infestation studies, duration of experiments), and this variation seems to be greater than the variation related to the characteristics of the study systems. Not surprisingly, applied studies considerably overestimate general effects due to both research and publication biases. The most critical research gap found in this analysis is the shortage of information on the effects of root herbivory on woody plants, especially on mature forest trees. Additionally, long-term studies employing nondestructive data collection methods are urgently needed to better understand the compensatory responses of plants to root herbivory.

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