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Abstract. 1. Several studies have shown that above- and belowground insects can interact by influencing each others growth, development, and survival when they feed on the same host-plant. In natural systems, however, insects can make choices on which plants to oviposit and feed. A field experiment was carried out to determine if root-feeding insects can influence feeding and oviposition preferences and decisions of naturally colonising foliar-feeding insects.

2. Using the wild cruciferous plant *Brassica nigra* and larvae of the cabbage root fly *Delia radicum* as the belowground root-feeding insect, naturally colonising populations of foliar-feeding insects were monitored over the course of a summer season.

3. Groups of root-infested and root-uninfested *B. nigra* plants were placed in a meadow during June, July, and August of 2006 for periods of 3 days. The root-infested and the root-uninfested plants were either dispersed evenly or placed in clusters. Once daily, all leaves of each plant were carefully inspected and insects were removed and collected for identification.

4. The flea beetles *Phyllotreta* spp. and the aphid *Brevicoryne brassicae* were significantly more abundant on root-uninfested (control) than on root-infested plants. However, for *B. brassicae* this was only apparent when the plants were placed in clusters. Host-plant selection by the generalist aphid *M. persicae* and oviposition preference by the specialist butterfly *P. rapae*, however, were not significantly influenced by root herbivory.

5. The results of this study show that the presence of root-feeding insects can affect feeding and oviposition preferences of foliar-feeding insects, even under natural conditions where many other interactions occur simultaneously. The results suggest that root-feeding insects play a role in the structuring of aboveground communities of insects, but these effects depend on the insect species as well as on the spatial distribution of the root-feeding insects.

Key words. Above–belowground interactions, *Brevicoryne brassicae*, *Delia radicum*, herbivore behaviour, multitrophic interactions, *Pieris rapae*, plant–insect interactions, plant selection.

Introduction

Traditionally, ecological studies that explore plant–insect interactions have been restricted to aboveground ecosystems, focusing on reciprocal interactions between plant shoots, foliar-feeding

insects, and their parasitoids (Turlings *et al.*, 1990; Barbosa *et al.*, 1991; Vet & Dicke, 1992; Harvey, 2005; Schoonhoven *et al.*, 2005). However, plants can act as vertical communication channels between insects that develop in the soil feeding on the roots, and foliar-feeding insects and their parasitoids. Root-feeding insects can thus act as potentially important participants of plant-based aboveground ecosystems (Van der Putten *et al.*, 2001; Wardle, 2002; Kaplan *et al.*, 2008; Soler *et al.*, 2008). Root-feeding insects can induce changes in the biomass and in the levels of primary and secondary compounds of plant shoots, and such changes can affect the survival, growth, and development of foliar-feeding insects that subsequently feed on the plant, as well as their parasitoids (Gange & Brown, 1989; Masters & Brown, 1992; Masters *et al.*, 1993; Bezemer *et al.*, 2003; Poveda et al., 2003; Soler *et al.*, 2005; Rasmann & Turlings, 2007; Soler *et al.*, 2007a, b; Wurst & van der Putten, 2007).

The effects of root-feeding insects on the performance of foliar-feeding insects are often highly association dependent (Johnson *et al.*, 2008). Some studies have found that the performance of foliar-feeding insects is enhanced in the presence of root herbivores (Gange & Brown, 1989; Masters & Brown, 1992; Masters, 1995; Poveda *et al.*, 2005), whereas others have shown a negative influence of root feeders on the growth and development of foliar feeders (Tindall & Stout, 2001; Bezemer *et al.*, 2003; Agrawal, 2004; Soler *et al.*, 2005; Van Dam *et al.*, 2005; White & Andow, 2006; Staley *et al.*, 2007). Furthermore, the growth and development of higher trophic level organisms, such as parasitoids and hyperparasitoids, can also be negatively affected by root herbivory (Soler *et al.*, 2005). Two broadly different mechanisms have been proposed to account for the positive and negative effects of root herbivory on their aboveground counterparts. The enhanced performance of foliar-feeding insects on plants containing root-feeding insects can be caused by increased concentrations of nutrients, such as nitrogen and other primary metabolites in the plant-shoots that are reallocated in response to root-attack (Gange & Brown, 1989; Masters *et al.*, 1993; Masters, 1995; Masters *et al.*, 2001). By contrast, the detrimental effects caused by root-feeding insects on the development of foliar-feeding insects and their parasitoids, can be as a result of increased levels of secondary plant compounds (phytotoxins) in the foliage following root herbivory (Bezemer *et al.*, 2004; Bezemer & van Dam, 2005; Soler *et al.*, 2005; Kaplan *et al.*, 2008).

Thus far, most research exploring above–belowground insect interactions has been performed under controlled conditions in a laboratory and/or greenhouse, whereby a root- and a foliar-feeding insect are forced to feed from the same individual plant. In these studies, a number of important fitness correlates of the foliar-feeding herbivores feeding from root-infested and root-uninfested plants are compared. In natural systems, however, insects are obviously not constrained and can make choices on which plants to oviposit and feed. More recently, it has been shown that root-feeding insects can influence behavioural decisions of the parasitoids of foliar-feeding insects, interfering in the host selection and the host preference of insect parasitoids (Masters *et al.*, 2001; Poveda *et al.*, 2005; Rasmann & Turlings, 2007; Soler *et al.*, 2007a, b). However, the influence of root-feeding insects on host-plant selection decisions of foliar-feeding insects, with which they potentially share the plant, has received little attention thus far.

Here, we examine whether and to what extent root-feeding insects influence host-plant selection of foliar-feeding insects in a natural environment, where a multitude of interactions takes place simultaneously. Groups of potted plants with and without root herbivores were placed into a meadow, and the number and species identity of naturally colonising insect herbivores feeding and/or ovipositing on both plant types were periodically recorded over a number of days. The model system consists of the wild cruciferous plant *Brassica nigra* and root-feeding larvae of the cabbage root fly *Delia radicum*. Previous studies on this model system have shown that the specialised foliar herbivore *Pieris brassicae* develop suboptimally on *B. nigra* plants infested by *D. radicum*, compared with root-uninfested plants. As the levels of a number of measured primary plant compounds were similar on root-infested and root-uninfested plants, the suboptimal performance of *P. brassicae* on root-infested plants was attributed to the high levels of secondary plant compounds (sinigrin) present on these plants (Soler *et al.*, 2005). We tested the hypothesis that the foliar-feeding insects prefer to feed and oviposit on root-uninfested plants rather than on root-infested plants, to optimise their performance and/or the performance of their offspring. *Delia radicum* prefers to oviposit on plants that have been previously damaged by conspecific larvae, often resulting in a clustered distribution of root-infested plants in the field (Baur *et al.*, 1996). Therefore, we also explored the effects of the spatial distribution of the root herbivores and their possible effects on host-plant selection by foliar-feeding herbivores. The experiment was consequently set-up with field plots containing plants that either had clustered or regular distributions of root-infested and root-uninfested plants.

Materials and methods

Biology

Black mustard, *Brassica nigra* L. (Brassicaceae), is a widely distributed annual wild crucifer that is common along rivers and other disturbed areas. Generally, this plant grows in extended patches and is often a dominant species in early succession habitats in the Netherlands (Schaminée *et al.*, 1998). Black mustard plants are attacked by several species of specialised root-feeding herbivores, including the cabbage root fly, *Delia radicum* L. (Diptera: Anthomyiidae) (Coaker & Finch, 1971). Aboveground shoots of *B. nigra* are usually attacked by only a few species of specialist and generalist herbivorous insects, most of which belong to the orders Hemiptera, Lepidoptera, and Coleoptera (Nielsen, 1977, 1978).

Plants and insect cultures

Delia radicum larvae were obtained from insect cultures maintained at the Laboratory of Ecobiology of Insect Parasitoids, of Rennes University, France, where they were cultured on roots of *B. napus* L. plants. *Brassica nigra* seeds were collected from a single population in Wageningen, the Netherlands. Seeds were surface sterilised and germinated on beds of glass-pearls (pearls of 1 mm diameter). One week after germination, seedlings were

transplanted into 1.2-l pots filled with sterilised potting soil. The plants were grown in a greenhouse at 22 ± 1 °C (day) and 16 ± 1 °C (night), 70% RH and L:D 16:8 h photoperiod. Natural daylight was supplemented by metal-halide lamps (225 μmol s⁻¹ m⁻² PAR). Plants were watered daily and only non-flowering plants were used in the experiments.

Experimental set-up

The manipulative field experiment was carried out between June and August of 2006. Within a meadow of approximately 1.5 Ha, a total of 160 individually potted *B. nigra* plants were arranged in four blocks (Fig. 1). Half of the plants were root-infested (by *D. radicum*) and half were root-uninfested, and served as a control. In each block, there were two plots with 20 plants each: 10 root-infested and 10 root-uninfested plants. In one of the two plots, root-infested and root-uninfested plants were regularly distributed, whereas in the other plot, root-infested and root-uninfested plants were placed in two clusters of root-uninfested plants and two clusters of root-infested plants (Fig. 1). For both distributions, the distance between adjacent plants was 1.2 m and the distance between the plots was 11 m. The experiment was repeated three times during the summer of 2006 (in June, July, and August) and new plants were used for each of these repetitions in time.

Prior to their use in the experiment, all plants were grown under controlled conditions in a greenhouse in 1.2-l pots filled with sterilised potting soil. 3 to 4 weeks after transplanting, six final instar (L3) *D. radicum* larvae were introduced into the pots and assigned to the root-infested treatment. This density was used, because it was previously found that *B. nigra* plants infested with six final instar (L3) *D. radicum* possess twice the concentration of phytotoxins in plant shoots when compared with uninfested plants, whereas the biomass of the plant shoots does not differ between the two treatments (Soler *et al.*, 2005). An important aim was to visually ensure that the experimental plants were similar in appearance and size, enabling the focus to be on the root herbivore-induced changes on the quality of the plant shoot. The root herbivore larvae were carefully placed with a small brush next to the main stem of the plant, and observed until they successfully crawled into the soil. After inoculation, the soil surface of each pot was carefully covered with gauze to prevent additional soil infestation by other insects. Seven days after inoculation, the plants were placed in the field.

In the field, each (potted) plant was placed at fixed positions in holes, such that the soil surface level of the potted plants was identical to the level of the soil surface of the field. The plants were kept in the field for a period of 3 days. Each day over this period, all plants were carefully checked and all insects and insect eggs present on the foliage of each plant were collected, and stored in 70% alcohol for subsequent identification. Immediately after terminating the experiment, ten randomly selected root-infested experimental plants were harvested to ensure that *D. radicum* larvae were present and actively feeding. The purpose of this inspection was to ensure that the root-damaged plants were indeed root-damaged. More than 80% of the larvae that were introduced were recovered.

Statistical analysis

The total number of insects after 3 days, classified by species, was analysed using generalised linear mixed models (GLMM)
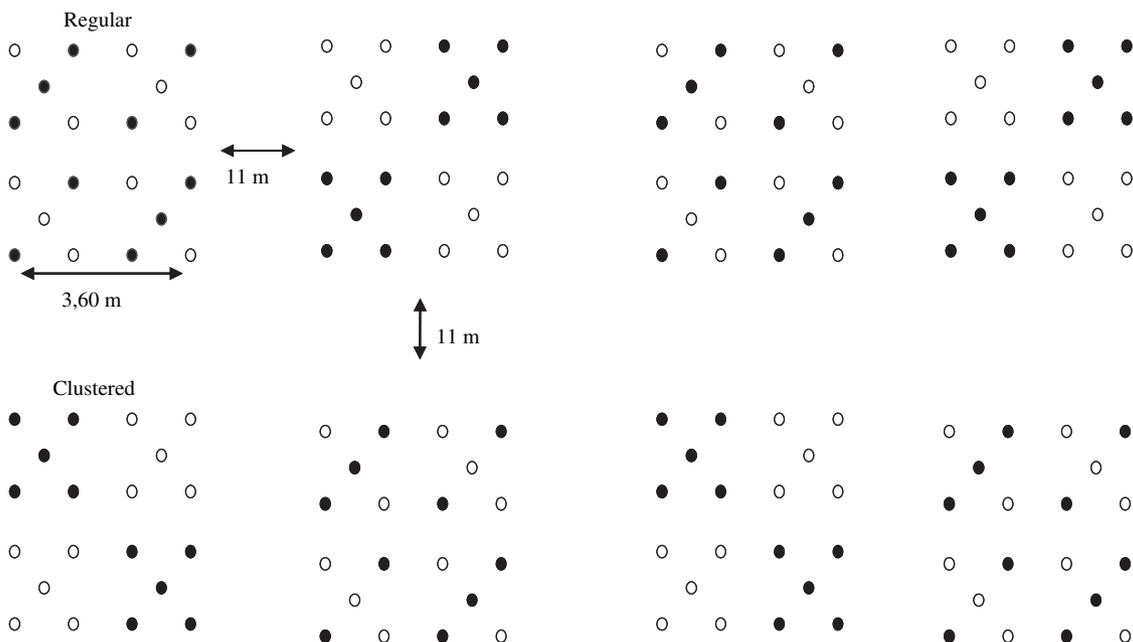

Fig. 1. Scheme of the experimental set-up. Groups of 160 plants were placed in the field in four blocks, in June, July and August 2006. White circles represent root-uninfested plants and black circles represent plants infested with *Delia radicum*. The root-infested and root-uninfested plants were distributed in patches either in clusters or regularly.
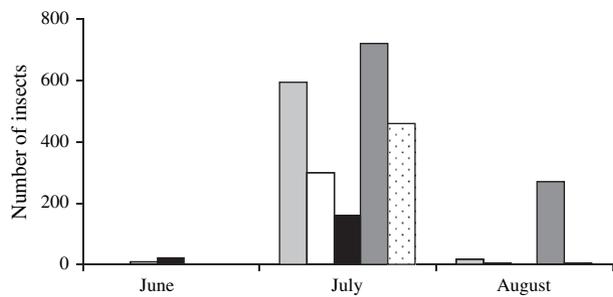
Fig. 2. Cumulative number of *Phyllotreta* spp. (light grey bars), *Brevicoryne brassicae* (white bars) and *Myzus persicae* (black bars), and eggs of *Pieris rapae* (dark grey bars) and *Chrysoperla carnea* (dotted bars), on the foliage of *Brassica nigra* plants during the 3 months in which the experiment was repeated.

with Poisson distribution and log link function, and the dispersion parameter estimated to correct for overdispersion. The model contained *Delia* infestation (root-infested or root-uninfested plants), the spatial distribution of root infested and uninfested plants (clustered or regular), and their interaction term as factors, with *Delia* infestation treatment being nested within spatial distribution in the blocked design (Fig. 1) as random terms, using GenStat 8.

Results

A total of 2581 insects and insect eggs were collected from the experimental *B. nigra* plants over the duration of the experiment. These insects were classified as adults of the flea beetle species *Phyllotreta* spp. (Coleoptera: Alticinae), adults and nymphs of the cabbage aphid *Brevicoryne brassicae* (Hemiptera: Aphidae) and the peach aphid *Myzus persicae* (Hemiptera: Aphidae), and eggs of the small cabbage white butterfly *Pieris rapae* (Lepidoptera: Pieridae). The differentiation at species level of *Phyllotreta undulata* and *P. diadema* could not be determined, and therefore these flea beetles, both of which are specialist foliar-feeding insects of cruciferous plants, were grouped together. With the exception of *M. persicae*, all of the observed species were specialised herbivores of plants in the Order Capparales (including the Brassicaceae). In addition to the herbivores, a generalist predator, the green lacewing *Chrysoperla carnea* (Neuroptera: Chrysopidae), was frequently observed on

the foliage of the experimental plants. More than 90% of the insects were collected during the second sampling date (July, Fig. 2), and subsequent analyses were, therefore, carried out for this collection date where the peak densities occurred.

The effects of the presence of root herbivores, and the distribution of the root-infested and root-uninfested plants on host-plant selection by aboveground insects differed between insect species (Table 1). The *Phyllotreta* spp. significantly preferred to feed on root-uninfested plants over root-infested plants, independent of the distribution of the plants (Fig. 3). The specialist aphid *B. brassicae* also significantly preferred to feed and reproduce on root-uninfested plants, but only when the root-infested and root-uninfested plants were arranged in clusters. Plant selection by the generalist aphid *M. persicae* was not influenced by the presence or the distribution of root-feeding insects (Table 1, Fig. 3), and neither was plant selection for oviposition by the specialist solitary butterfly *P. rapae* (Fig. 3). Furthermore, oviposition preference of the generalist insect predator *C. carnea* was not significantly influenced by the presence or absence of root herbivores. Significantly fewer eggs of the generalist predator, however, were found in clustered than in regular plots (Table 1, Fig. 4).

Discussion

Our results in a natural environment show that plant selection by foliar-feeding insects can be influenced by root-feeding insects. It is remarkable that two of the most abundant foliar-feeding insects of *B. nigra*, the flea beetles *Phyllotreta* spp. and the aphid *B. brassicae*, significantly preferred to feed and oviposit on the shoots of root-uninfested plants rather than on the shoots of root-infested plants. In previous studies, we found that the levels of foliar phytotoxins (glucosinolates) of root-infested *B. nigra* plants by *D. radicum* are more than twice as high as compared with root-uninfested plants, and the specialised foliar herbivore *P. brassicae* develop suboptimally on these plants (Soler *et al.*, 2005). Therefore, root-infested *B. nigra* plants may represent a suboptimal nutritional source for other species of foliar herbivores. Considering that *Delia* spp. commonly attack brassicaceous plants, foliar herbivores of these plants may be under strong selection pressure to avoid ovipositing or feeding on plants with *Delia* spp, particularly if this is correlated with a significant reduction in their fitness, and root-uninfested plants are readily available.

Table 1. Wald-tests for the fixed effects from generalized linear mixed models (GLMM) and corresponding *P*-values associated with the effect of root herbivory by *Delia radicum* (RH: presence versus absence), and the spatial distribution of root-infested plants (D: regular or clustered) on the number of *Phyllotreta* spp., *Brevicoryne brassicae* and *Myzus persicae*, and eggs of *Pieris rapae* and *Chrysoperla carnea* on *Brassica nigra* plants.

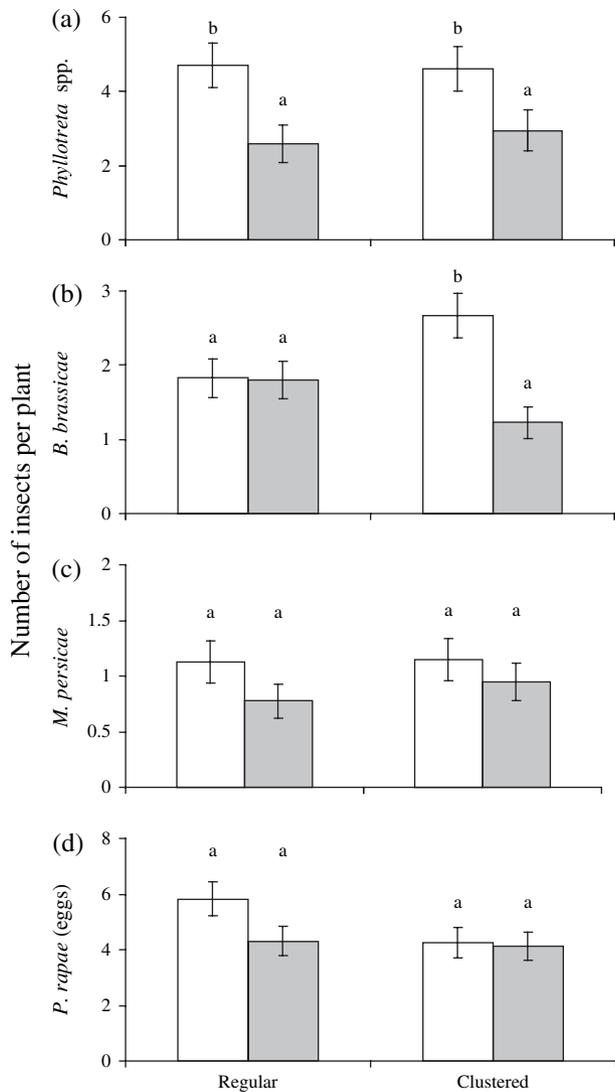| Factors	d.f.	*Phyllotreta* spp.		*B. brassicae*		*M. persicae*		*P. rapae*		*C. carnea*	
		F	P	F	P	F	P	F	P	F	P
Distribution (D)	1	0.04	0.83	0.26	0.61	0.33	0.56	2.46	0.11	8.73	0.003
Root herbivory (RH)	1	8.53	0.003	7.35	0.007	2.39	0.12	2.53	0.11	1.42	0.23
RH * D	1	0.14	0.70	6.62	0.01	0.27	0.60	1.28	0.25	0.04	0.84

Fig. 3. GLMM back transformed estimates (±SE) of the number of insects on root-uninfested (white bars) and root-infested (grey bars) plants. Plots had either a regular or a clustered distribution of root-infested and root-uninfested plants. Although there are no interactive effects between root herbivore presence and spatial distribution for most of the insect species, data is shown for both factors separately.

Fig. 4. GLMM back transformed estimates (±SE) of the number of eggs per plant of the predator *Chrysoperla carnea*, in the foliage of *Brassica nigra* plants. White bars represent root-uninfested plants and grey bars represent root-infested plants. Plots had either a regular or a clustered distribution of root-damaged and root-undamaged plants. Although there is no interaction effect, data are shown for both factors separately.

Interestingly, the specialist aphid *B. brassicae* preferred to feed on root-uninfested plants only when root-uninfested and root-infested plants were arranged in clusters. It is possible that root-infested plants placed in clusters emit a stronger and more concentrated odour plume, signalling more clearly the presence of root herbivores belowground. In that case, *B. brassicae* could have detected whilst in flight, the stronger volatile signal emitted from the plant clusters with root herbivores, and thus avoided these plants when selecting feeding and reproductive sites. However, unlike larger insects with stronger flight capabilities, aphids generally disperse according to the direction of the prevailing winds (Compton, 2002). Furthermore, *B. brassicae* is thought to possess post-alighting host recognition behaviour and
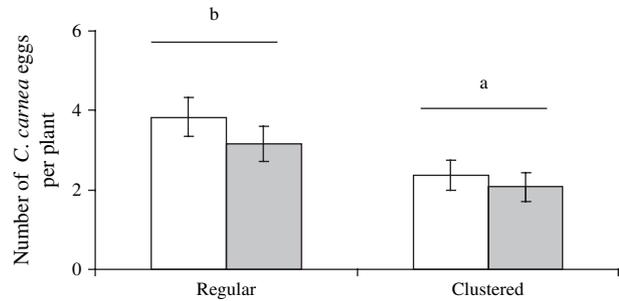
uses contact cues from the plant after landing on the foliage to determine their suitability (Bukovinszky *et al.*, 2005), rather than exhibiting strong pre-alighting plant recognition mediated by plant volatiles. It has previously been reported that not only the presence or absence, but also the density of root herbivores feeding on a plant can be a crucial factor in generating a cascade of effects in the aboveground insects (Soler *et al.*, 2005). This result shows that the spatial distribution of root-feeding insects can also affect the outcome of the interaction.

In contrast with *B. brassicae* and *Phyllotreta* spp., butterflies of the specialised *P. rapae* did not discriminate between root-infested and root-uninfested plants, and laid similar numbers of eggs on both plants. Host-plant selection might be an important behavioural decision for the adults of this species, because the newly emerged larvae poses limited dispersal capacity. It will remain feeding in the plant selected by the butterfly in the early developmental phase. However, bearing in mind that *P. rapae* is a solitary species that usually lays only a single egg per plant, it is possible that it is less selective for differences in plant quality within plant species, and the solitary larvae compensate for feeding in a nutritionally suboptimal plant, by feeding a larger amount of biomass (Davies & Gilbert, 1985). We did not examine, however, if the larvae emerging from the eggs laid on root-infested plants, migrate to neighbouring plants when reaching instars that posses higher mobility, looking for plants not 'occupied' with root-feeding insects. It is also possible that the costs and benefits of developing on root-infested or root-uninfested plants are small in this species.

The only generalist herbivore that was abundant on *B. nigra* plants was the green peach aphid *M. persicae*, and this species did not discriminate between root-infested and root-uninfested plants. This species is known to feed on hundreds of host-plant species distributed over 30 different families, and to colonise wide areas (Weber *et al.*, 1986). Therefore, it is not surprising that this aphid species did not discriminate between relatively subtle chemical differences within the shoot of root-infested and root-uninfested plants of the same plant species.

Oviposition preference of the carnivorous insect *C. carnea* was also not influenced by the presence or absence of root-feeding

insects on the plants. The larvae of chrysopids are predators that feed on aphids and young larvae of various species of beetles, butterflies and moths, as well as many other insects (Pree *et al.*, 1989). Chrysopid larvae prefer to attack mobile prey and are very active during their entire juvenile period. The predatory larvae are not restricted to the plant where they emerge, but instead disperse and forage for prey on adjacent plants (Pree *et al.*, 1989). Therefore, in *C. carnea* and other chrysopid species, oviposition decisions by the adult female may have little effect on the development and fitness of their offspring. Consequently, it is unlikely that host-plant quality is a major selection pressure in the oviposition of these predators.

In summary, this study shows that feeding and oviposition preferences of two specialist herbivores of *B. nigra* plants, differ according to the presence or absence of belowground herbivores and their distribution in the field. The preference of these insect species for root-uninfested plants to feed and oviposit further, shows that belowground insects can interact with their aboveground counterparts in natural environments. It is possible that such interactions allow insect species inhabiting spatially separated domains, but sharing the same host-plant species, to optimize their performances. Despite an increasing awareness of the importance of root-feeding insects in ecological studies (Van der Putten *et al.*, 2001; Wardle, 2002; Bardgett & Wardle, 2003; Hunt-Joshi & Blossey, 2005; Kaplan *et al.*, 2008), belowground processes are still often not considered when evaluating the factors that shape the structure and function of plant-insect communities. Field studies integrating above- and belowground organisms, exploring multi-trophic multi-species plant-insect interactions will help to facilitate a better understanding of the importance and magnitude of the interactions between insects within the below- and aboveground domain.

Acknowledgements

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