



## Original article

# The presence of root-feeding nematodes – Not AMF – Affects an herbivore dispersal strategy



Annelies De Roissart<sup>a,\*</sup>, Eduardo de la Peña<sup>a</sup>, Lien Van Oyen<sup>a</sup>, Thomas Van Leeuwen<sup>b</sup>, Daniel J. Ballhorn<sup>c</sup>, Dries Bonte<sup>a</sup>

<sup>a</sup> Ghent University, Dep. Biology, Terrestrial Ecology Unit, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium

<sup>b</sup> Ghent University, Dep. Crop Protection, Laboratory of Agrozoology, Coupure Links 653, B-9000 Ghent, Belgium

<sup>c</sup> Portland State University, Dep. of Biology, 1719 SW 10th Ave, Portland, OR 97201, USA

## ARTICLE INFO

## Article history:

Received 13 May 2013

Accepted 15 July 2013

Available online 19 August 2013

## Keywords:

Dispersal

Plant–herbivore interaction

Soil biota

*Tetranychus urticae*

## ABSTRACT

Plant quality and aboveground herbivore performance are influenced either directly or indirectly by the soil community. As herbivore dispersal is a conditional strategy relative to plant quality, we examined whether belowground biotic interactions (the presence of root-feeding nematodes or arbuscular mycorrhizal fungi) affect aerial dispersal of a phytophagous mite (*Tetranychus urticae*) through changes in performance of their host plant (*Phaseolus vulgaris*). Aerial dispersal strategies of mites were analyzed in wind-tunnel experiments, in which a unique mite pre-dispersal behavior (rearing) was assessed in relation to the presence of belowground biota on the host plant on which mites developed. Spider mite pre-dispersal behavior significantly increased with the experienced mite density on the host during development. Additionally, plants infected with root-feeding nematodes induced an increase of spider mite aerial dispersal behavior. The results highlight that belowground herbivores can affect population dynamics of aboveground herbivores by altering dispersal strategies.

© 2013 Elsevier Masson SAS. All rights reserved.

## 1. Introduction

Dispersal, the movement of organisms away from their natal habitat, affects individual fitness, but also population dynamics, population genetics and species distribution (Bowler and Benton, 2005; Clobert et al., 2009). Consequently, dispersal is a key process in ecology as well as in evolutionary and conservation biology (Kokko and Lopez-Sepulcre, 2006; Ronce, 2007). Dispersal strategies are known to be shaped by selection pressures related to the spatial arrangement of habitat, kin competition and inbreeding avoidance (Bowler and Benton, 2005). Additionally, proximate factors related to, for instance, habitat quality and population density, are known to increase emigration from patches of adverse quality (Clobert et al., 2009; De Meester and Bonte, 2010). Environmental conditions experienced during development, not just those experienced during the dispersal phase, affect the body condition of an animal (Benard and McCauley, 2008) and as such

the costs of dispersal (Bonte et al., 2012). Thus, such environmental conditions influence how far or how often individuals move away from their place of birth.

The habitat of small herbivores is mainly determined by the host plant on which they feed and live. Plants are known to respond to herbivore attack with the expression of various defense strategies. These traits range from chemical defenses, for instance alkaloids or herbivore-induced volatiles, to mechanical defenses such as trichomes or tough cuticles (Baldwin, 1991; Bezemer and van Dam, 2005; Ballhorn et al., 2013a). Since plants are composed of interconnected organs, biotic interactions at specific plant regions are expected to induce strong effects on plant quality and the subsequent trophic interactions throughout all regions of the plant (Bezemer and van Dam, 2005; Ohgushi, 2005; van Dam and Heil, 2011). A prominent example of these plant-mediated trophic interactions is the link between the aboveground herbivores and mutualistic or antagonistic biota associated with roots (Wardle et al., 2004; De Deyn and Van der Putten, 2005; Hartley and Gange, 2009; Koricheva et al., 2009; Thamer et al., 2011). Interactions between above- and belowground plant herbivores are known to be complex. Positive, negative and neutral effects in both directions have been demonstrated (Masters, 1995; Tindall and Stout, 2001; Blossey and Hunt-Joshi, 2003; De Deyn et al., 2007). Interactions between plant mutualists, such as arbuscular

\* Corresponding author. Tel.: +32 9 264 52 13; fax: +32 9 264 87 94.

E-mail addresses: [Annelies.Deroissart@ugent.be](mailto:Annelies.Deroissart@ugent.be) (A. De Roissart), [Eduardo.delapena@ugent.be](mailto:Eduardo.delapena@ugent.be) (E. de la Peña), [Lien.Vanoyen@ugent.be](mailto:Lien.Vanoyen@ugent.be) (L. Van Oyen), [Thomas.Vanleeuwen@ugent.be](mailto:Thomas.Vanleeuwen@ugent.be) (T. Van Leeuwen), [Ballhorn@pdx.edu](mailto:Ballhorn@pdx.edu) (D.J. Ballhorn), [Dries.Bonte@ugent.be](mailto:Dries.Bonte@ugent.be) (D. Bonte).

mycorrhizal fungi (AMF), and aboveground biota result in a positive plant response in most cases (Hoffmann et al., 2009). However, depending on the feeding guild and host specialization of the herbivore, AMF can also have a neutral or negative effect on the plant (Graham and Abbott, 2000; Reynolds et al., 2006; Sudova and Vosatka, 2008; Hartley and Gange, 2009; Koricheva et al., 2009). Previous studies indicate that belowground-induced changes in host quality can affect population dynamics of foliar herbivores by altering individual growth rates and population sizes of such aboveground herbivores (Awmack and Leather, 2002; van Dam et al., 2003; Hoffmann et al., 2009; Bonte et al., 2010). Changes in plant quality and plant chemistry caused by the induction of direct and indirect defense mechanisms may additionally induce signaling through the production of volatiles and as such impact behavioral aspects of foliar herbivores (Dicke, 2000; Ballhorn et al., 2013b).

The suitability of host plants for herbivores does not only depend on the intrinsic nutritional quality of the plants, but also on the presence and density of con- and heterospecific herbivores (Ohgushi, 2005). When increased local densities of herbivores lead to an enhanced depletion of resources, exploitative competition will be strong (Klomp, 1964) and local density may act as a source of information to adjust dispersal strategies (De Meester and Bonte, 2010). Previous studies have shown emigration propensity to increase with density for a variety of taxa (Bowler and Benton, 2005; De Meester and Bonte, 2010), including two-spotted spider mites (Li and Margolies, 1993b) that are subject of this study.

Two-spotted spider mites (*Tetranychus urticae* Koch; Acari: Tetranychidae) are generalist cell-content sucking herbivores (Helle and Sabelis, 1985) that feed on leaf parenchyma of a wide variety of plant species belonging to many different families. Due to their wide host range, severe feeding damage and rapid population growth these herbivores are a pest to many crops (Yano and Takafuji, 2002; Van Leeuwen et al., 2010). Spider mites have evolved a well-developed dispersal technique of aerial (long distance) dispersal (Osakabe et al., 2008) that is easily quantified under laboratory conditions as it is initiated by a unique pre-dispersal behavior, termed “rearing” (Li and Margolies, 1993a, 1994). Rearing entails orientating away from light sources and stretching of the forelegs (Osakabe et al., 2008). Previous studies demonstrated a strong underlying genetic component of this dispersal strategy (Li and Margolies, 1993a; Li and Margolies, 1994 for *Tetranychus*; Jia et al., 2002 for a predatory mite). The controlling proximate factors for changes in dispersal were host plant senescence, population density and aerial humidity (Li and Margolies, 1993b).

In the present study, the impact of belowground biota on the density-dependent aerial dispersal strategies of aboveground spider mites was examined. We applied two belowground treatments: herbivory by root-feeding nematodes (*Pratylenchus penetrans*; Tylenchida: Pratylenchidae) and the symbiosis with arbuscular mycorrhizal fungi (*Glomus* spp.; Glomerales: Glomaceae) (hereafter referred to as AMF). Dispersal strategies of spider mites were evaluated using wind-tunnel experiments. In a previous studies, in which the prevalence of local adaptation on spider mites was tested (Bonte et al., 2010), belowground nematodes induced water stress in host plants and induced a significant overall decrease in fitness (i.e. growth rate) in spider mites. Considering these results, increased levels of dispersal are expected, and more specifically an increased level of pre-dispersal behavior in these herbivores should be observed when mites are reared on plants infected with belowground living nematodes. A shift in the positive density-dependency of aerial dispersal is anticipated if nematodes induce changes in food quality and lower the overall carrying capacity on plant leaves. Since no effect of AMF on mite fitness was previously

observed (Bonte et al., 2010), levels of dispersal in spider mites are not expected to change when reared on plants that have established this belowground symbiosis.

## 2. Material and methods

### 2.1. The model system

#### 2.1.1. Plant treatments

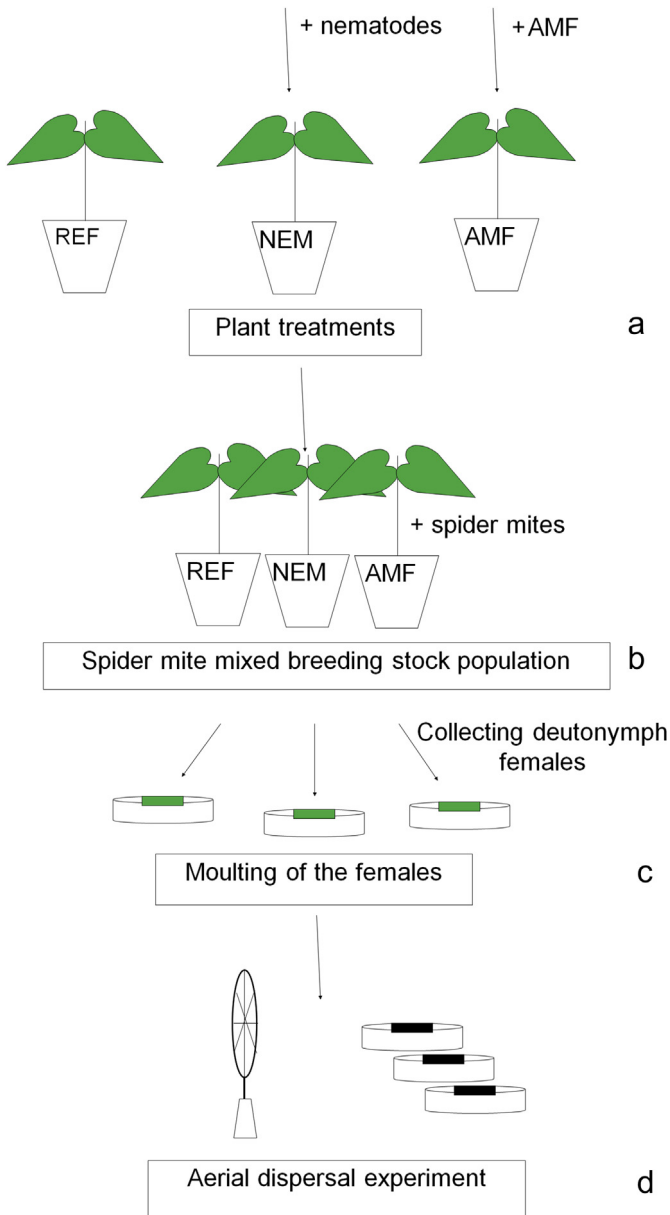
We used common bean or snap bean (*Phaseolus vulgaris* L.; Fabales: Fabaceae) as host plant in our experiments. Beans were grown in 5 liter trays (15 × 15 × 35 cm; 15 plants/tray) under greenhouse conditions (25 °C; 16:8 LD photoperiod) in commercial standard potting soil (Structural™ Type 0; containing 1.25 g/m<sup>3</sup> of 14–16–18 N–P–K fertilizer) that was sterilized by autoclaving (120 °C, 120 min, 1 atm) as a control treatment. Two experimental treatments were applied, in which plant parasitic nematodes *P. penetrans* (Tylenchida: Pratylenchidae) or a mixture of arbuscular mycorrhizal fungi (AMF) (*Glomus* spp.; Glomerales: Glomaceae) were added to the sterilized substrate (Fig. 1). Around 5000 *Pratylenchus* individuals (commercial inoculum; hzpc research B.V.) were added per plant-tray and allowed to establish a population on the beans for one month. In the AMF treatment, plants were inoculated by watering plant-trays with 500 ml of demineralized water containing 1 g of spore blend of *Glomus* spp. (commercial mycorrhizal inoculums; MycoGrow™) and the symbiosis was allowed to establish for one month (according to the manufactures protocol). This resulted in consistent root colonization of the bean plants by *Glomus* spp. All trays were watered twice per week with tap water. After one month, plants were transferred to growth chambers for inoculation with mites.

#### 2.1.2. Validation of treatments

Levels of infection by AMF and root nematodes were verified in experimental plants at the end of the experiment. The substrate was removed from the roots by washing with water. Roots of 27 plants per treatment were cut in 1 cm fragments and nematodes were subsequently extracted using the Baermann funnel technique over a period of 96 h. This resulted in on average 1.31 ± 0.75 nematodes/g of soil and 44.3 ± 12.2 nematodes/g root. For AMF colonization, root samples were processed the same way and fragments were stained following the technique of Vierheilig et al. (1998) after cutting. Root samples were investigated using the technique of Giovannetti and Mosse (1980) using an Olympus microscope. The AMF treatment resulted in an average root infection of (21 ± 7%, n = 27). No nematode infections were observed in plants from the sterile and AMF treatments and no hyphae were observed in plants from the sterile and the nematode treatments.

#### 2.1.3. Establishment of an experimental population of spider mites

A genetically diverse population of two-spotted spider mites (Van Leeuwen et al., 2008) that has been kept in stock culture on snap bean (*P. vulgaris* L.) since 2000 was used to establish an experimental mite population. In order to obtain mites from plants of all treatments, a mix of 30 bean plants, containing 10 plant individuals from each of the three treatments was used for the experimental population (Fig. 1). Each plant individual was potted separately to avoid mixing of belowground treatments. Every third week, before all plants died due to herbivory, a random subsample of mites was used to inoculate the next mixture of bean plants. Local adaptation towards one of the three treatments was avoided by (i) the diffusive spread of the adult mites over the plants from the inoculation point, (ii) the heterogeneous bean stock with respect to belowground treatment and (iii) random inoculation events and the lack of any preference–performance correlation in



**Fig. 1.** Course of the experiments. a: plant treatment; b: set-up of the mite breeding stock population; c: moulting of the selected deutonymph females; d: aerial dispersal experiment using wind-tunnel.

relation to the considered plant types (Bonte et al., 2010; unpub. data). Mites for the dispersal experiments were sampled from the different plant types in this heterogeneous stock population.

## 2.2. Host plant performance

To analyze the impact of nematodes or AMF on plant performance, we used 10 two-week old bean plants from every belowground treatment (of the same growth stage as the plants provided to the mites). Above- and belowground biomass were measured after drying the plants for 40 h in an air-flow oven at 70 °C. For another three bean plants, nitrogen content was analyzed by ISO 5983-2 standards following the Kjeldahl method and measured with a continuous flow analyzer (Foss Fiastar 5000). Phosphorus-content was analyzed by colorimetry (EC L279/15 20.12.71) (A more detailed methodology is provided in the [Supplementary material](#)).

Three subsamples from each plant were taken for chemical analyses. Water content of shoots and roots was calculated from the relative difference between fresh and dry weight. Bean plants from the genus *Phaseolus* commonly show a variety of nitrogen- and carbon-based plant defenses. We tested whether cyanogenic precursors were present in plant tissue (Ballhorn et al., 2011), but all plant individuals tested were not cyanogenic (see also Bonte et al., 2010).

## 2.3. Aerial dispersal protocol

### 2.3.1. Selection of dispersive females

One or two days after mating *T. urticae* females disperse aerially (Li and Margolies, 1994). In order to obtain females of the same age, available quiescent deutonymph (1 day before adult emergence) females were transferred from each plant type of the breeding stock population to a mite-free 1 cm × 1 cm bean leaf disc of the same plant type as from which they were collected. Spider mites do not move during development. Therefore the plant of collection resembles the plant of development (Fig. 1). Three guarding males per female were added in order to guarantee mating immediately after molting of females to the adult stage. The leaf discs were placed with the abaxial face upwards in Petri dishes (diameter 4 cm) on wet cotton to avoid wilting and prevent mites from escaping. Leaf discs were stored in a growth chamber (16:8 day:night light regime, 60% RH, 25 °C). Prior to mite transfer for the aerial dispersal assay, we recorded mite density (average number of individuals per cm<sup>2</sup>) on the leaf from which the mites were collected. All mites collected from the same leaf were analyzed together and considered as one unit of replication in our statistical analyses.

### 2.3.2. Aerial dispersal assay

To evaluate the effect of our treatments and mite density on rearing dispersal behavior, mated females were transferred to test arenas. These dispersal tests were conducted from October 2008–April 2009 on a total of 1158 mites within a total of 28 test days comprising of more than 180 h of observation. We applied the same setup as used by Li and Margolies (1993a, 1994). The test arenas consisted of 1 cm<sup>2</sup> black painted plastic discs placed on soaked cotton dishes in order to prevent mites from escaping. Depending on the number of available mites, between one and ten individuals from one leaf (from plants with one of the three belowground treatments) were placed on one cm<sup>2</sup> disc [no effects of mite densities on the test dishes were observed during test trials ( $F_{1,135} = 0.95$ ;  $P = 3325$ )]. We applied an upward (30°) wind current of 1.5 m/s (produced by a fan) to the test arenas with and a strong light source (990 lumen) at the source of the air current. As mites perform rearing behavior before entering the air column, we were able to count and select the number of mites performing this behavior (for at least 5 s) in the subsequent 3 h. Mites that showed this behavior were immediately removed in order to avoid pseudo-replication. We simultaneously tested mites derived from plants of all three treatments.

## 2.4. Statistical analyses

All plant performance parameters were averaged per plant individual and subsequently analyzed using ANOVA with treatment as independent factor. Generalized linear mixed models (GLMM) for binomially distributed data with logit-link and correction for potential overdispersion were used to analyze the proportion of mites displaying rearing behavior. In these logistic regressions, the number of mites that showed the pre-dispersal behavior relative to the total number of tested mites from one leaf was the dependent factor. Independent factors were “total mite density on the leaf of development” (continuous factor) and the “treatment of the host plant”. In order to control for possible correlation due to the

common date of testing, we included “date” as a random effect. Because of this random error structure, we visualized the modeled regression instead of multiple regression lines for each day when tests were performed. In addition, rearing frequencies for subsamples were plotted when consisting of more than 10 tested mites in order to minimize scatter from small subsamples with low weight in the entire regression analysis. Effective degrees of freedom in all analyses were estimated by Satterthwaite procedure (Verbeke and Molenberghs, 2000). All analyses were performed with SAS 9.1 (Proc Glimmix; SAS Institute, 2001).

### 3. Results

#### 3.1. Host plant performance

The belowground treatment had a significant effect on the plant biomass allocation and nutritional composition (Table 1). Nematodes and AMF had a detrimental effect on total and shoot biomass (Fig. 2a). Nematodes also decreased root biomass in comparison to plants that were grown with AMF and sterile substrate (Fig. 2a). Root biomass allocation (i.e. the root/shoot ratio) was higher in AMF plants ( $0.44 \pm 0.08$  SE) than in plants from the nematode ( $0.14 \pm 0.02$  SE) and the sterile-substrate ( $0.14 \pm 0.03$  SE) treatments. N and P concentration were lower in the control than in nematode or AMF treated plants (Fig. 2c). Water content for roots averaged  $86.23\% \pm 0.60\%$  SE overall treatments (no significant differences among treatments were observed;  $F_{2,27} = 2.18$ ;  $P = 0.138$ ). Shoot water content was an average of 3% lower in plants treated with nematodes compared to plants from the sterile-substrate treatment (Fig. 2b) (Table 1).

#### 3.2. Aerial dispersal

The probability for an individual female mite to perform the rearing dispersal behavior increased with increasing mite density on the host ( $\beta = 0.021 \pm 0.007$ ;  $F_{1,126} = 8.39$ ;  $P < 0.005$ ). This positive density-dependence was independent of the treatment (interaction density  $\times$  treatment  $F_{3,123} = 1.21$ ;  $P = 0.310$ ), but overall rearing probabilities depended on the host treatment ( $F_{2,126} = 5.53$ ;  $P = 0.005$ ; see Fig. 3). Mites that developed on plants inoculated with nematodes showed a higher rearing probability compared to mites from the sterile treatment (Fig. 4; Tukey's test:  $t_{126} = 3.27$ ;  $P = 0.004$ ). Treatment with AMF had no effect on the mite rearing dispersal behavior (differences in the two other pairwise combinations were not significant; Tukey's test:  $t_{126} < 1.81$ ;  $P > 0.05$ ).

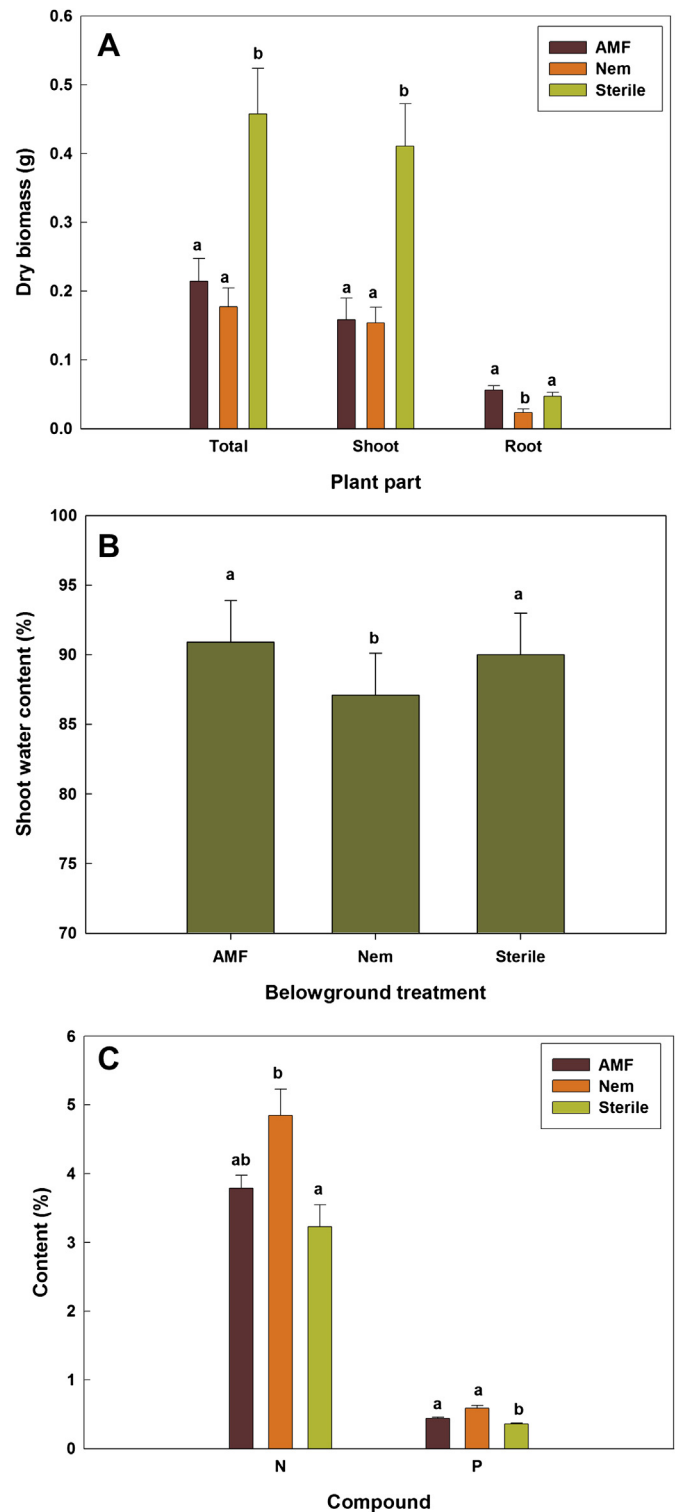
### 4. Discussion

It is generally acknowledged that a change in the belowground community structure can affect plant performance and population

**Table 1**

Results of ANOVA of the measured plant biomass and plant quality variables in relation to the belowground treatment.

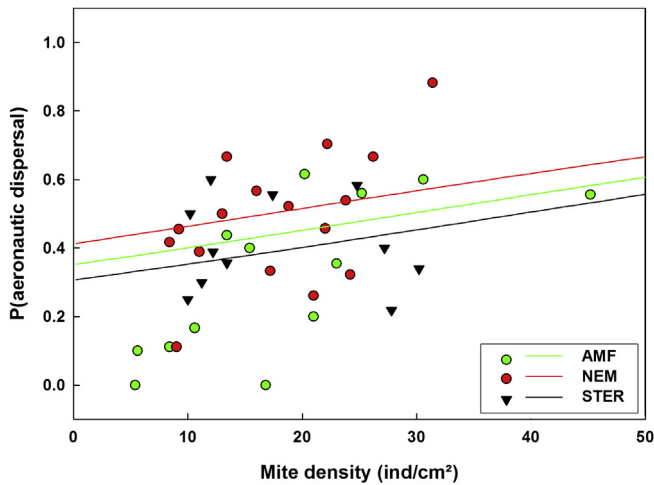
Dependent variable	F	P
Total biomass (g)	12.44	<0.0001
Aboveground biomass (g)	13.69	<0.0001
Belowground biomass (g)	8.86	<0.0001
Root/shoot ratio	11.26	<0.0001
Root water content (%)	2.18	0.138
Shoot water content (%)	42.95	<0.0001
N-content (% dry weight)	7.09	0.026
P-content (% dry weight)	17.81	0.003



**Fig. 2.** Effects of the belowground biotic treatment on plant performance. A: plant dry biomass; B: shoot water content; C: N and P-content. Equal notations indicate non-significant contrast for the respective plant performance measurements. Error bars represent standard errors.

growth of aboveground herbivores (Wardle et al., 2004; De Deyn and Van der Putten, 2005; Kaplan et al., 2008; Hoffmann and Schausberger, 2012), with cascading effects on higher trophic levels (Van der Putten et al., 2001). Prevailing mechanisms behind these plant-mediated multitrophic interactions are diverse, but

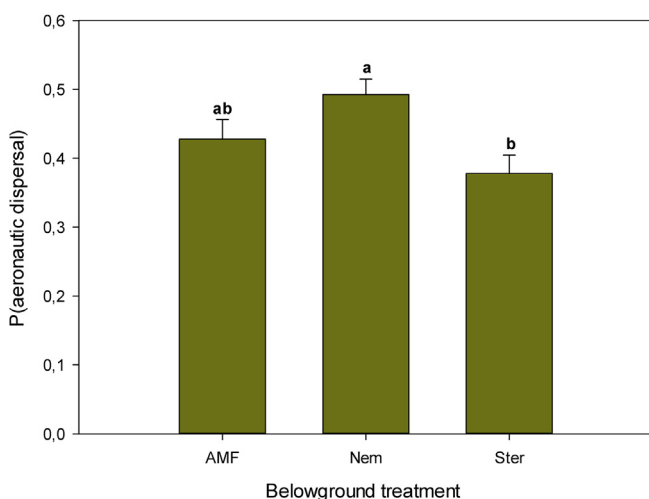




**Fig. 3.** Effects of density and soil treatments on the aerial dispersal behavior. Proportions of mites performing pre-aerial dispersal behavior in relation to its experienced density on the host and the host belowground treatment (AMF: green, NEMATode: red or STERile: black). Notice that frequencies are plotted in the graph as dots (independent of the total number of tested individuals) but that individual behavior (whether pre-dispersal behavior occurred or not) was modeled as a binomial variable. We omitted data points with less than ten tested mites according to density from the figure to enhance visibility of the observed pattern. Lines indicate predictions derived from the binomial mixed model. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

these mechanisms are always mediated through changes in host plant quality and/or the up-regulation of plant defense strategies (Masters and Brown, 1997; Van der Putten et al., 2001). The complexity of these interactions is, however, enormous and depends on variation in abiotic conditions at both temporal and spatial scales (Wardle et al., 2004; Vandegehuchte et al., 2010; Thamer et al., 2011). The impact of belowground biota on oviposition and feeding behavior of foliar herbivores has been demonstrated by Anderson et al. (2011). Here, we document the impact of belowground biota on the dispersal behavior of aboveground herbivores for the first time.

Rearing rates for aerial dispersal were positively associated with the mite population density on the source leaf. This corresponds to



**Fig. 4.** Overall effects of soil treatments on the aerial dispersal behavior. Proportions of mites performing pre-aerial dispersal behavior in relation to the host belowground treatment for the overall average density of  $19.35 \pm 0.66$  SE mites. Equal notations indicate non-significant contrast. Error bars represent standard errors.

previous findings of positive density-dependent strategies in vertebrates (Matthysen, 2005) and invertebrates (De Meester and Bonte, 2010; Bitume et al., 2013) and stresses the need to consider the intraspecific competition as a proximate driver of individual dispersal (Clobert et al., 2009). In the case of passive dispersal strategies, costs of dispersal are very high (Bonte et al., 2012). However, if habitat quality decreases, costs of philopatry will exceed those of dispersal and an induction of high dispersal rates is expected (Travis et al., 1999; Hovestadt et al., 2001; Kun and Scheuring, 2006).

No detectable effect of AMF on mite fitness (Bonte et al., 2010) and dispersal were observed despite a significant decrease of biomass in plants treated with AMF. The observed neutral to negative effect of AMF on plant performance might be due to the use of young 2-week old bean plants (Johnson et al., 1997). In the first weeks following germination, plants obtain their necessary resources from seed reserves. In this stage, the loss of carbon to the fungus decreases allocation to photosynthesis or defense and AMF can become parasitic (Johnson et al., 1997). Because dispersal evolves as an alternative behavioral strategy to philopatry, both strategies should have equal fitness expectations (Clobert et al., 2009; Bonte et al., 2012). As such, while some plant quality parameters were affected by this treatment, they appear not to impact the mite's future fitness (Bonte et al., 2010) and therefore do not have a strong impact on the aerial dispersal strategy.

In nematode infected plants, dispersal propensity was anticipated to increase under high mite population densities due to a decrease of plant quality or an increased production of defensive compounds, thereby lowering the mite carrying capacity. Aerial dispersal was, however, higher in mites that developed on nematode-treated hosts. Increased dispersal of spider mites therefore appears to be caused by their development on plants with belowground nematode herbivory. This belowground interaction resulted in decreased water content and/or the production of unidentified defensive metabolites. Because no change in the density threshold has been observed, increased dispersal rates are regarded as a response to future fitness costs when staying on a host of subordinate quality (Bonte et al., 2010) due to, for instance, the production of secondary defense metabolites (van Dam et al., 2005). In our experiment, no declines in nutritional plant tissue quality were detected (Bonte et al., 2010) nor detectable levels of cyanogenic potential in nematode treated plants (Ballhorn et al., 2007). Total nitrogen-content is known to be a poor predictor of nutritional plant quality (Awmack and Leather, 2002; Schoonhoven et al., 2005). The absence of cyanogenic glycosides does not rule out the prevalence of hitherto unidentified nitrogen-containing defensive metabolites (e.g. alkaloids or tannins) which in some cases reduce digestive efficiency of arthropod herbivores and may have caused the increased dispersal response.

Shoot water content was systematically lower in plants treated with nematodes. A decrease in shoot water content due to root herbivory has previously been described as mechanism negatively affecting aboveground herbivore presence and performance (Erb et al., 2009, 2011). Since plant structural and biochemical parameters changed in multiple and non-correlated ways after treatment with belowground biota, we were not able to assign one exact plant trait to be the driving force for the observed change in dispersal potential, and likely, the response is due to multiple, mutually interacting changes in plant quality.

In conclusion, our study demonstrates that plant growth is negatively affected by AMF and nematode infection of the roots. Since only nematode herbivory affected the overall level of aerial dispersal, without a shift in density dependency, we attribute specific changes in plant quality like water turgor, but potentially also other factors, as the proximate cause of the increased aerial

dispersal rates. Because such effects were not found for AMF, our results demonstrate that at least some specific belowground biotic interactions in the plant rhizosphere affect dispersal of aboveground herbivores. Soil biotic interactions may consequently affect the dispersal strategies of aboveground herbivores and their eventual spatial population dynamics (Sackett et al., 2010).

## Acknowledgments

This project was funded by FWO projects G.0610.11. TvL and EdIP are a post-doctoral research fellow of the Research Foundation Flanders (Belgium) (FWO). AdR is funded by BOF-Ugent. DB was supported by the FWO research network Eve-Net (Eco-Evolutionary dynamics). Startup funds to D.J. Ballhorn from Portland State University are gratefully acknowledged. We thank Stefanie Kautz and Adrienne L. Godschalx (Portland State University) for language editing and critical reading of the manuscript.

## Appendix A. Supplementary material

Supplementary data related to this article can be found online at <http://dx.doi.org/10.1016/j.actao.2013.07.005>.

## References

- Anderson, P., Sadek, M.M., Wackers, F.L., 2011. Root herbivory affects oviposition and feeding behavior of a foliar herbivore. *Behavioral Ecology* 22, 1272–1277.
- Awmack, C.S., Leather, S.R., 2002. Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology* 47, 817–844.
- Baldwin, I.T., 1991. Damage-induced alkaloids in wild tobacco. In: Raupp, M.J., Tallamy, D.W. (Eds.), *Phytochemical Induction by Herbivores*, pp. 47–69.
- Ballhorn, D.J., Pietrowski, A., Heil, M., Lieberei, R., 2007. Quantitative effects of cyanogenesis on an adapted herbivore. *Journal of Chemical Ecology* 33, 2195–2208.
- Ballhorn, D.J., Kautz, S., Jensen, M., Schmitt, I., Heil, M., Hegeman, A.D., 2011. Genetic and environmental interactions determine plant defences against herbivores. *Journal of Ecology* 99, 313–326.
- Ballhorn, D.J., Godschalx, A.L., Kautz, S., 2013a. Co-Variation of chemical and mechanical defenses in lima bean (*Phaseolus lunatus* L.). *Journal of Chemical Ecology* 39, 413–417.
- Ballhorn, D.J., Kautz, S., Schädler, M., 2013b. Induced plant defense via volatile production is dependent on rhizobial symbiosis. *Oecologia*. <http://dx.doi.org/10.1007/s00442-012-2539-x>. Epub ahead of print.
- Benard, M.F., McCauley, S.J., 2008. Integrating across life-history stages: consequences of natal habitat effects on dispersal. *American Naturalist* 171, 553–567.
- Bezemer, T.M., van Dam, N.M., 2005. Linking aboveground and belowground interactions via induced plant defenses. *Trends in Ecology & Evolution* 20, 617–624.
- Bitume, E.V., Bonte, D., Ronce, O., Bach, F., Flaven, E., Olivieri, I., Nieberding, C.M., 2013. 2013. Density and genetic relatedness increase dispersal distance in a subsoil organism. *Ecology Letters* 16, 430–437.
- Blossey, B., Hunt-Joshi, T.R., 2003. Belowground herbivory by insects: influence on plants and aboveground herbivores. *Annual Review of Entomology* 48, 521–547.
- Bonte, D., De Roissart, A., Vandegehuchte, M.L., Ballhorn, D.J., Van Leeuwen, T., de la Pena, E., 2010. Local adaptation of aboveground herbivores towards plant phenotypes induced by soil biota. *PLoS One* 5, e11174.
- Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V.M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T.G., Chaput-Bardy, A., Clobert, J., Dytham, C., Hovestadt, T., Meier, C.M., Palmer, S.C.F., Turlure, C., Travis, J.M.J., 2012. Costs of dispersal. *Biological Reviews* 87, 290–312.
- Bowler, D.E., Benton, T.G., 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews* 80, 205–225.
- Clobert, J., Le Galliard, J.F., Cote, J., Meylan, S., Massot, M., 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12, 197–209.
- De Deyn, G.B., Van der Putten, W.H., 2005. Linking aboveground and belowground diversity. *Trends in Ecology & Evolution* 20, 625–633.
- De Deyn, G.B., van Ruijven, J., Raaijmakers, C.E., de Ruiter, P.C., van der Putten, W.H., 2007. Above- and belowground insect herbivores differentially affect soil nematode communities in species-rich plant communities. *Oikos* 116, 923–930.
- De Meester, N., Bonte, D., 2010. Information use and density-dependent emigration in an agrobiont spider. *Behavioral Ecology* 21, 992–998.
- Dicke, M., 2000. Chemical ecology of host-plant selection by herbivorous arthropods: a multitrophic perspective. *Biochemical Systematics and Ecology* 28, 601–617.
- Erb, M., Flors, V., Karlen, D., de Lange, E., Planchamp, C., D'Alessandro, M., Turlings, T.C.J., Ton, J., 2009. Signal signature of aboveground-induced resistance upon belowground herbivory in maize. *Plant Journal* 59, 292–302.
- Erb, M., Kollner, T.G., Degenhardt, J., Zwahlen, C., Hibbard, B.E., Turlings, T.C.J., 2011. The role of abscisic acid and water stress in root herbivore-induced leaf resistance. *New Phytologist* 189, 308–320.
- Giovannetti, M., Mosse, B., 1980. Evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. *New Phytologist* 84, 489–500.
- Graham, J.H., Abbott, L.K., 2000. Wheat responses to aggressive and non-aggressive arbuscular mycorrhizal fungi. *Plant and Soil* 220, 207–218.
- Hartley, S.E., Gange, A.C., 2009. Impacts of plant symbiotic fungi on insect herbivores: mutualism in a multitrophic context. *Annual Review of Entomology* 54, 323–342.
- Helle, W., Sabelis, M.W. (Eds.), 1985. *Spider Mites: Their Biology, Natural Enemies, and Control*. Elsevier, Amsterdam, p. 458.
- Hoffmann, D., Vierheilig, H., Riegler, P., Schausberger, P., 2009. Arbuscular mycorrhizal symbiosis increases host plant acceptance and population growth rates of the two-spotted spider mite *Tetranychus urticae*. *Oecologia* 158, 663–671.
- Hoffmann, D., Schausberger, P., 2012. Plant-mediated aboveground-belowground interactions: the spider mite perspective. *Acarologia* 52, 17–27.
- Hovestadt, T., Messner, S., Poethke, H.J., 2001. Evolution of reduced dispersal mortality and 'fat-tailed' dispersal kernels in autocorrelated landscapes. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268, 385–391.
- Jia, F., Margolies, D.C., Boyer, J.E., Charlton, R.E., 2002. Genetic variation in foraging traits among inbred lines of a predatory mite. *Heredity* 89, 371–379.
- Johnson, N.C., Graham, J.H., Smith, F.A., 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytologist* 135, 575–586.
- Kaplan, I., Halitschke, R., Kessler, A., Sardanelli, S., Denno, R.F., 2008. Constitutive and induced defenses to herbivory in above- and belowground plant tissues. *Ecology* 89, 392–406.
- Klomp, H., 1964. Intraspecific competition and the regulation of insect numbers. *Annual Review of Entomology* 9, 17–40.
- Kokko, H., Lopez-Sepulcre, A., 2006. From individual dispersal to species ranges: perspectives for a changing world. *Science* 313, 789–791.
- Koricheva, J., Gange, A.C., Jones, T., 2009. Effects of mycorrhizal fungi on insect herbivores: a meta-analysis. *Ecology* 90, 2088–2097.
- Kun, A., Scheuring, I., 2006. The evolution of density-dependent dispersal in a noisy spatial population model. *Oikos* 115, 308–320.
- Li, J., Margolies, D.C., 1993a. Quantitative genetics of aerial dispersal behavior and life-history traits in *Tetranychus urticae*. *Heredity* 70, 544–552.
- Li, J.B., Margolies, D.C., 1993b. Effects of mite age, mite density, and host quality on aerial dispersal behavior in the 2-spotted spider-mite. *Entomologia Experimentalis et Applicata* 68, 79–86.
- Li, J.B., Margolies, D.C., 1994. Responses to direct and indirect selection on aerial dispersal behavior in *Tetranychus urticae*. *Heredity* 72, 10–22.
- Masters, G.J., 1995. The impact of root herbivory on aphid performance – field and laboratory evidence. *Acta Oecologica – International Journal of Ecology* 16, 135–142.
- Masters, G.J., Brown, V.K., 1997. Host-plant mediated interactions between spatially separated herbivores: effects on community structure. In: *Multitrophic Interactions in Terrestrial Systems*, pp. 217–237.
- Matthysen, E., 2005. Density-dependent dispersal in birds and mammals. *Ecography* 28, 403–416.
- Ohgushi, T., 2005. Indirect interaction webs: herbivore-induced effects through trait change in plants. *Annual Review of Ecology Evolution and Systematics* 36, 81–105.
- Osakabe, M., Isobe, H., Kasai, A., Masuda, R., Kubota, S., Umeda, M., 2008. Aerodynamic advantages of upside down take-off for aerial dispersal in *Tetranychus* spider mites. *Experimental and Applied Acarology* 44, 165–183.
- Reynolds, H.L., Vogelsang, K.M., Hartley, A.E., Bever, J.D., Schultz, P.A., 2006. Variable responses of old-field perennials to arbuscular mycorrhizal fungi and phosphorus source. *Oecologia* 147, 348–358.
- Ronce, O., 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology Evolution and Systematics* 38, 231–253.
- Sackett, T.E., Classen, A.T., Sanders, N.J., 2010. Linking soil food web structure to above- and belowground ecosystem processes: a meta-analysis. *Oikos* 119, 1984–1992.
- Schoonhoven, L.M., van Loon, J.J.A., Dicke, M., 2005. *Insect-Plant Biology*, second ed. Oxford University Press, Oxford, 421.
- Sudova, R., Vosatka, M., 2008. Effects of inoculation with native arbuscular mycorrhizal fungi on clonal growth of *Potentilla reptans* and *Fragaria moschata* (Rosaceae). *Plant and Soil* 308, 55–67.
- Thamer, S., Schädler, M., Bonte, D., Ballhorn, D.J., 2011. Dual benefit from a belowground symbiosis: nitrogen fixing rhizobia promote growth and defense against a specialist herbivore in a cyanogenic plant. *Plant and Soil* 341, 209–219.
- Tindall, K.V., Stout, M.J., 2001. Plant-mediated interactions between the rice water weevil and fall armyworm in rice. *Entomologia Experimentalis et Applicata* 101, 9–17.
- Travis, J.M.J., Murrell, D.J., Dytham, C., 1999. The evolution of density-dependent dispersal. *Proceedings of the Royal Society of London Series B-Biological Sciences* 266, 1837–1842.
- van Dam, N.M., Harvey, J.A., Wackers, F.L., Bezemer, T.M., van der Putten, W.H., Vet, L.E.M., 2003. Interactions between aboveground and belowground induced responses against phytophages. *Basic and Applied Ecology* 4, 63–77.
- van Dam, N.M., Raaijmakers, C.E., van der Putten, W.H., 2005. Root herbivory reduces growth and survival of the shoot feeding specialist *Pieris rapae* on *Brassica nigra*. *Entomologia Experimentalis et Applicata* 115, 161–170.

- van Dam, N.M., Heil, M., 2011. Multitrophic interactions below and above ground: en route to the next level. *Journal of Ecology* 99, 77–88.
- Van der Putten, W.H., Vet, L.E.M., Harvey, J.A., Wackers, F.L., 2001. Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends in Ecology & Evolution* 16, 547–554.
- Van Leeuwen, T., Vanholme, B., Van Pottelberge, S., Van Nieuwenhuyse, P., Nauen, R., Tirry, L., Denholm, I., 2008. Mitochondrial heteroplasmy and the evolution of insecticide resistance: non-Mendelian inheritance in action. *Proceedings of the National Academy of Sciences of the United States of America* 105, 5980–5985.
- Van Leeuwen, T., Vontas, J., Tsagkarakou, A., Dermauw, W., Tirry, L., 2010. Acaricide resistance mechanisms in the two-spotted spider mite *Tetranychus urticae* and other important Acari: a review. *Insect Biochemistry and Molecular Biology* 40, 563–572.
- Vandeghechuchte, M.L., de la Pena, E., Bonte, D., 2010. Relative importance of biotic and abiotic soil components to plant growth and insect herbivore population dynamics. *PLoS One* 5, e12937.
- Verbeke, G., Molenberghs, G., 2000. *Linear Mixed Models for Longitudinal Data*. Springer-Verlag, New-York, p. 568.
- Vierheilig, H., Coughlan, A.P., Wyss, U., Piche, Y., 1998. Ink and vinegar, a simple staining technique for arbuscular-mycorrhizal fungi. *Applied and Environmental Microbiology* 64, 5004–5007.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. *Science* 304, 1629–1633.
- Yano, S., Takafuji, A., 2002. Variation in the life history pattern of *Tetranychus urticae* (Acari: Tetranychidae) after selection for dispersal. *Experimental and Applied Acarology* 27, 1–10.