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Original article

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

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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.

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 though 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

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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 predispersal 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^3 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