



Research Paper

Crop cultivar affects performance of herbivore enemies and may trigger enhanced pest control by coaction of different parasitoid species



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ABSTRACT

Pest control by naturally occurring predators and parasitoids is an ecosystem service that may benefit from greater diversity of the pest's natural enemies. Co-occurrence of different enemy species, which act as service providers, can increase or stabilize pest control. Simultaneous cultivar diversity in varietal mixtures might foster such service providers, and the diverse cultivars might finally profit from occurrence of different natural enemies. Here, we tested how the ecosystem service pest control may be influenced by different crop cultivars and by the action of different parasitoid species. We investigated naturally occurring control of an apple pest, the apple blossom weevil *Anthonomus pomorum* (Curculionidae), by the parasitoid wasp species *Scambus pomorum* (Ichneumonidae) and *Bracon variator* (Braconidae) on five different cultivars (genotypes) of domestic apple *Malus domestica* in an organic orchard ecosystem. We quantified parasitism of the apple blossom weevil on the apple cultivars at three different times during the pest's development period. We evaluated whether apple cultivar and pest developmental status lead to comparable or to divergent parasitism patterns by different wasp species. We further assessed size and sex ratio of the wasps to estimate their performance and biocontrol potential on different cultivars. We found that pest parasitism was increased and homogenized across cultivars by coaction of the two wasp species, which belong to the same guild and contributed differently to parasitism – (i) with progressing time and (ii) on the different cultivars. Furthermore, female size differed significantly between cultivars for both wasp species, and it followed the preference-performance hypothesis for *S. pomorum*, where it was positively related to parasitism. Repeated sampling revealed that only the last sampling (shortly before adult weevil emergence) provides a complete estimate of effective parasitism by both wasp species. In conclusion, intraspecific variation among crop cultivars can result in divergent performance of parasitoids, and it may trigger enhanced pest control through different parasitoid species. The coaction of different species may thus contribute to maximization and stabilization of pest control in heterogeneous cropping systems.

1. Introduction

Key ecosystem services like pollination or pest control can be increased or stabilized by higher species richness (biodiversity) of service-providing species (Straub et al., 2008; Brose and Hillebrand, 2016; Zhao et al., 2016). Increased services, for example higher levels of pollination or pest regulation, are expected when service-providing species differ in their qualitative and quantitative contribution to the service (Blüthgen and Klein, 2011; Blitzer et al., 2016). Stabilized services, for example persistent control of a pest organism under variable environmental conditions, are expected when the same level of service is provided by different species that may replace each other

(Yachi and Loreau, 1999; Blüthgen and Klein, 2011; Macfadyen et al., 2011).

Control of crop pests by naturally occurring enemies such as parasitoids or predators represents an important ecosystem service (Losey and Vaughan, 2006; Rusch et al., 2015). Pests are usually controlled by a suite of natural enemies that may be related to different instars or stages of the pest, or occur in different habitats or in different seasons (Tylianakis and Romo, 2010). The performance and effectiveness (i.e. biocontrol potential) of the pests' natural enemies can be substantially influenced by plant traits (Cortesero et al., 2000; Ode, 2006; Collatz and Dorn, 2013). These plant traits, either chemical or physical, may vary intraspecifically due to environmental conditions

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such as nutrient and water availability (Huberty and Denno, 2004; Chen et al., 2010; Gutbrodt et al., 2011), or due to plant genetic differences (Sarraz et al., 2008; Stoeckli et al., 2009; Smith and Clement, 2012). Genetic differences between cultivars of the same plant species (Miller and Gross, 2011; Kettenring et al., 2014), and resulting differences in traits between cultivars, often affect performance and effectiveness of pests and their enemies (Newton et al., 2009; Santolamazza-Carbone et al., 2014; Mody et al., 2015). Simultaneous presence of different cultivars should thus substantially increase opportunities for natural enemies to contribute to pest control in a given agroecosystem (Newton et al., 2009; Chateil et al., 2013).

To elucidate the role of biodiversity for the ecosystem service pest control in agroecosystems, the variation of traits between cultivars and its effect on natural enemies may be used to investigate the relevance of co-occurrence of different species of service providers on a particularly fine scale. Here it will be possible to explicitly test plant intraspecific variation and well-characterized enemy species and pest stages.

A particularly important group of natural enemies for many agricultural pests are hymenopteran parasitoids (Letourneau et al., 2009; Macfadyen et al., 2015). These parasitoids, either naturally present in agro-ecosystems or released as biological control agents, may help to considerably reduce pest populations (Schmidt et al., 2003; Bale et al., 2008). For pest control by parasitoids, species diversity may be especially important, because different parasitoid species may attack different host instars or stages (Traynor and Mayhew, 2005; Martinou and Wright, 2007), search for hosts on different plant species or plant parts (Feng et al., 2015), or be active at different times of the season (Sorribas et al., 2010). In addition to species diversity, population characteristics such as sex ratio can strongly influence the biocontrol potential of parasitoids. Here, an increase in proportion of females is generally considered as beneficial for biological control (Ode and Hardy, 2008; Wajnberg et al., 2016).

In this study, we focused on an organic orchard ecosystem with various cultivars of apple trees, a flower herbivore (apple blossom weevil, *Anthonomus pomorum*, Curculionidae) and its naturally occurring parasitoids (*Scambus pomorum*, Ichneumonidae; *Bracon variator*, Braconidae; *Pteromalus varians*, Pteromalidae). Apple trees are infested by a number of pest species that challenge apple production from early to late season (Cross et al., 1999). The apple blossom weevil *A. pomorum* is an early season pest that causes damage to developing apple buds (Toepfer et al., 1999). Developing weevils are attacked by several parasitoid wasps, which are prevalent early in season and reach parasitism levels of up to 50% (Cross et al., 1999). The most abundant species in the UK and probably also in Central Europe is the ichneumonid *S. pomorum* (Alford, 1984). Furthermore, the braconid *B. variator* and the pteromalid *P. varians* have been reported to parasitize developing larvae and/or pupae of *A. pomorum* in Swiss apple orchards (Mody et al., 2011). Besides a few studies on the life-cycle and winter survival of *S. pomorum* (Zijp and Blommers, 1992, 2002) as well as parasitoid association with certain apple cultivars (Mody et al., 2011) and apple species (Knuff et al., 2017), information on the multitrophic relationships between different parasitoids, the host *A. pomorum* and the food plant apple is scarce.

To test whether and how the ecosystem service pest control on different crop cultivars may be affected by the action of different parasitoid species, we addressed the following hypotheses: (1) *Parasitism rate as well as parasitoid size and sex ratio (as measures of parasitoid performance) change with collection date.* We repeated sampling of flower buds infested by the host herbivore *A. pomorum* three times during the immature period of *A. pomorum* to assess the phenology of parasitism, and to determine an optimized point in time for estimation of effective parasitism rate and parasitoid performance. (2) *Apple cultivar influences overall pest parasitism and individual contributions of parasitoid species involved.* We compared parasitism rates of *A. pomorum* on different apple cultivars for total parasitism and specifically for parasitism by *S. pomorum* and *B. variator* to test whether

Table 1
Overview of studied apple cultivars.

Cultivar	Bloom time	Reference
Discovery	Early	Paprštein and Blazek (1996)
Retina	Mid-early	Kellerhals et al. (2003)
Ariwa	Mid-late	Kellerhals et al. (2003)
Florina	Mid-late	Bodor and Toth (2008)
Rewena	Late	Bodor and Toth (2008)

hosts on different cultivars are differentially parasitized. (3) *Parasitoid performance is influenced by apple cultivar and reflects parasitism patterns.* We quantified parasitoid size and sex ratio as measures of parasitoid performance and biocontrol potential for different cultivars, and tested whether the parasitoids' performance is related (a) to their incidence on apple cultivars according to the preference-performance hypothesis (e.g., Desneux et al., 2009) and (b) to the weight of their weevil hosts.

2. Materials and methods

2.1. Study trees

This study was conducted in an organic orchard on five apple cultivars differing in bloom time (Table 1) in Northern Switzerland (47° N, 8° E, elevation around 450 m). Apple cultivars are propagated vegetatively through grafting (Cornille et al., 2012), thus they represent well-defined genotypes and thereby provide a consistent basis for investigating complex multitrophic interactions. Studied trees were apple dwarf trees (2.0–3.5 m height, 6–18 years old) grafted on M9 (Gelber Metzger-Paradiesapfel) rootstocks. Tree rows were aligned in North-South direction and distances between trees and rows of trees were 1.5–2 m and 4.5 m, respectively. For more details on trees see (Mody et al., 2015). For the study, we randomly chose 20 trees per cultivar.

2.2. Sampling of infested buds (capped blossoms)

Apple blossom weevils colonize apple trees at the early bud stages (Toepfer et al., 2002; Piskorski and Dorn, 2010) and lay eggs into the flower buds. Hatched weevil larvae destroy the flower organs and lead to the formation of so-called “capped blossoms” that consist of the flower base and the dry petals wrapped around the developing weevil. Based on regular monitoring of weevil development, we chose three points in time for collection of capped blossoms according to the approximate proportion of weevils that had reached the pupal stage at that time (collection 1: 50% of weevils at pupal stage, May 3; collection 2: 75%, May 7; collection 3: 95%, May 14). On each of the collection dates, we sampled randomly one third of the total amount of capped blossoms from each tree. We stored all the capped blossoms separated per tree and collection date in Petri dishes (14 cm diameter) with a circular filter paper and with the lid secured by rubber bands. We changed the filter paper regularly to reduce humidity and to avoid mold formation. Petri dishes were kept under outside conditions but protected from frost and direct sunlight.

2.3. Wasp characteristics

We examined the Petri dishes containing the capped blossoms at 24 h intervals for freshly emerged weevils (Mody et al., 2015) and wasps. We removed all the emerged insects and immediately deep-froze them in Eppendorf tubes. Parasitoids were dried at 40 °C for 48 h and then weighed as a proxy of the parasitoids' body size (Mody et al., 2012). We determined parasitoid species and sex (visible by presence or absence of an ovipositor). Both parasitoid size and sex ratio were considered as measures of parasitoid performance, with large body size

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