

Host plant genotype determines bottom-up effects in an aphid-parasitoid-predator system

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Abstract

Plant genotypes are known to affect performance of insect herbivores and the community structure of both herbivores and higher trophic levels. Still, only a limited number of studies demonstrate differences in the performance of predators and parasitoids because of plant genotypic effects and most of these focus on gall formers. We designed a greenhouse experiment to investigate the effects of host plant genotype on fitness components in a grass-aphid-carnivore system. We used clones of quackgrass [*Elytrigia repens* (L.) Desv. ex Nevski (Poaceae)], the aphid *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae), the parasitoid wasp *Aphidius colemani* (Viereck) (Hymenoptera: Braconidae), and the predatory lacewing *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae). The number of aphid offspring differed considerably among plant genotypes. These differences were only in part because of differences in the production of biomass among host genotypes. Therefore, genotypes may differ in their nutritional value for phytophages. The number of aphids attacked by the parasitoid also differed among genotypes and aphid numbers only partly accounted for this effect. Moreover, pupal development time of female parasitoids was affected by plant genotype. We found no differences in mortality, body size, or sex ratio of hatching wasps between genotypes of quackgrass. Development time of the larvae and larval weight of the predatory lacewings differed among genotypes, but not weight of pupae and adults. Generally, the proportion of the total variance explained by the plant genotype was smaller for parasitoids and predators than for aphids. Overall, our experiments indicated that the plant genotype affects tri-trophic interactions, but also that the strength of these effects decreases along the food chain.

Introduction

The distribution, abundance, and performance of insect herbivores are affected by intraspecific variability in quality of their host plants (Karban, 1992; Rossi & Stiling, 1998; Cronin & Abrahamson, 1999; Awmack & Leather, 2002; Ruhnke et al., 2006, 2009). Within plant species and populations, environmental differences may lead to spatial and temporal variation in the quality of host plants for herbi-

vores and their natural enemies (Rossi & Stiling, 1998; Moon et al., 2000; Kagata et al., 2005). Furthermore, host quality also depends on differences between the genotypes of the plant, including differences in morphological traits, nutrient contents, and the concentration of secondary compounds (Levin, 1973; Rausher, 1981; Rossiter et al., 1988; O'Reilly-Wapstra et al., 2007). This variability affects the performance of herbivores feeding on different genotypes (Cronin & Abrahamson, 1999; Underwood & Rausher, 2000; Hughes et al., 2008).

Herbivores in turn are the basic resources for parasitoids and predators. Therefore, distribution, abundance, and performance of parasitoids and predators should also depend in some way on the quality of the host plant of their prey (Bottrell et al., 1998; Havill & Raffa, 2000; Awmack & Leather, 2002; Giles et al., 2002; Harvey et al., 2003). If the population dynamics of parasitoids or insect

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predators depend on the host quality of the attacked insects (Lill et al., 2002), differences in the quality among the prey's host plants will in turn affect the top-down control of herbivores (Hunter, 2003). Overall, differences in quality between plant individuals may have complex consequences for the structure and dynamics of food webs associated with plants (Underwood & Rausher, 2000; Wimp et al., 2005; Bailey et al., 2006; Crutsinger et al., 2006).

Studies into the influence of host plant genotype on the performance of parasitoids and predators are still scarce and predominantly conducted on gall-forming herbivores and their enemies (Johnson, 2008). Furthermore, studies on genotypic effects in tri-trophic interactions usually concentrated on the diversity and structure of the communities of predators and parasitoids (Fritz, 1995; Wimp et al., 2005; Johnson, 2008), and experimental studies investigating the effects of host plant genotype on the performance of parasitoids and predators focussed on crop and ornamental plants (Hare & Luck, 1991; Fuentes-Contreras et al., 1998; Sarfraz et al., 2008). However, a defence system modified by artificial selection, as in the case of crop or ornamental plants, may lead to effects which are difficult to generalize to natural systems (Gols et al., 2008a,b; Gols & Harvey, 2009). Although some studies demonstrated already effects of host plants on natural enemies of herbivores via changed host quality (Harvey et al., 2007; Gols et al., 2008a,b) and chemical signals (Thaler, 2002; Wu & Baldwin, 2009) there are still few investigations of how natural genotypic variability of plants affects the performance of these third-level consumers. Predators and parasitoids may not only be less directly affected by the quality of the host plant than herbivores, but also differ from each other by their feeding mode and their confinement to their prey feeding on the plant. Thus, species of the third trophic level may track genetic variation of plants quite differently from herbivores and may further show different responses within their trophic level (Wimp et al., 2005).

Plants, phloem-sucking herbivores, and koinobiont parasitoids, allowing their hosts to continue development after being parasitized, form a widespread tri-trophic system. However, the importance of genotypic differences under controlled conditions have, to the best of our knowledge, not been analysed in studies in such systems. To fill this gap, we designed an experiment to assess the performance of an aphid, a parasitoid, and a predator species on various genotypes of the clonal common quackgrass, *Elytrigia (Agropyron) repens* (L.) Desv. ex Nevski (Poaceae). Clonal plants are a major component of many vegetation types (de Kroon & van Groenendael, 1997) and have been shown to exhibit considerable genotypic vari-

ability of traits which may affect associated organisms (Rossi & Stiling, 1998; Cronin & Abrahamson, 1999; Underwood, 2009). Our experiment posed the following specific questions: (1) do plant genotypes affect the performance of herbivores leading to differences in the population size of the herbivores among host genotypes? And (2) do these differences translate into differences in the performance of parasitoids and predators?

Materials and methods

Study species, sampling of genotypes, and plant propagation

Elytrigia repens is a perennial grass with a broad ecological niche. It is highly competitive and spreads by long, branching rhizomes, which allow the propagation of numerous replicates of single genotypes (Leakey & Chancellor, 1977). Beside this clonal growth, the self-sterile quackgrass reproduces sexually through wind-pollinated outcrossing (Werner & Rioux, 1977). In July 2003, we sampled seeds from five randomly selected plant individuals from different sites across an area of about 10 km² near Bad Kösen (51°8'N, 11°43'O; Saxony-Anhalt, Germany) with a distance of 800 m between the two closest sites. Seeds of one plant were sampled per site. Seeds were sown in standard soil. One randomly selected seedling from each sampled plant individual was transferred to a large pot (60 × 40 × 30 cm) filled with a mix of standard potting soil and sand (2:1, vol/vol). These five genotypes were cultivated in a greenhouse at a temperature of 15–25 °C and 14 h day length. We supplied additional light by high-pressure sodium lamps (400 W, Son-T Agro; Philips, Hamburg, Germany). Every 2 months, plants were cut to a height of about 5 cm to prevent flowering and promote clonal growth. There were no obvious differences regarding plant and leaf morphology between the genotypes.

Parasitoid experiment

In May 2005, rhizomes of each genotype were harvested and cut into pieces of 20–50 mm. Each piece had at least two buds. These cuttings were then planted in shallow trays and placed in the greenhouse. Once grass shoots reached a height of about 5 cm, individual ramets of each genotype were transplanted separately into polyvinyl chloride (PVC) tubes (diameter 10 cm, height 20 cm, closed at the bottom with 100 µm mesh) filled with a 1:1 (vol/vol) mixture of standard potting soil and sand. A translucent PVC ring (height 20 cm) was attached at the top of the tubes to minimize light competition between plants and dispersal of aphids. Each genotype was replicated 12×, leading in total to 60 pots. Furthermore, we constructed six cages (60 × 40 × 100 cm) covered with nylon gauze (200 µm mesh size) and equipped with a hook- and

loop-fastener in front of each cage to allow entrance into the cage. For each genotype two tubes were placed in every cage, giving a total of 10 tubes per cage. Tubes were randomly distributed within cages.

After 1 month, five nymphs of the bird cherry-oat aphid *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae) from a laboratory culture on maize were added to each of the 60 tubes. This aphid is a heteroecious, holocyclic species with sexual stages. *Prunus padus* (L.) is the primary host and various grasses, including *E. repens* as well as certain cereal crops, are secondary hosts. Although aphids are quite sessile organisms, the PVC ring may have not completely prevented dispersal between the genotypes. Only very few alates could be found (<1%). Therefore, aphid numbers can be regarded as integrative measure of genotype quality and aphid reproduction. Further after a period of 1 month, newly hatched females and males (10 each) of the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae), bought from Sautter and Stepper (Ammerbach, Germany), were introduced into each cage. The first mummies (indicating the beginning of pupal development of parasitoids) appeared after 12 days. In the next 7 days, every plant was checked once a day for mummies and we carefully removed the mummies from leaves. Number of mummies was recorded and we placed mummies in Petri dishes according to date of appearance and experimental unit (tube). Petri dishes were kept at 20 °C and L14:D10 photoperiod. Dishes were checked once or twice a day. Emerged parasitoids were counted, sexed, and stored in alcohol. Thorax length was measured using a binocular scope (Zeiss Stemi SV11; Carl Zeiss AG, Jena, Germany) as an indicator of body size (see Demmon et al., 2009). Aboveground biomass of the plants was harvested, dried to weight constancy, and numbers of aphids per plant were counted.

Predator experiment

For each genotype of *E. repens*, three pots (15 cm diameter, 14 cm depth) were planted with five ramets per pot (giving a total of 15 plants). After establishment of ramets, five late-instar *R. padi* were added. The pots were randomly arranged in the greenhouse. To prevent aphid escape, all pots were enclosed with a tent of nylon gauze with a 200 µm mesh. Newly hatched larvae of the lacewing *Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae), bought from Sautter and Stepper, were individually placed on moist filter paper in plastic Petri dishes (9 cm diameter, 1.5 cm deep), randomly assigned to one *E. repens* genotype, and placed in a climate chamber maintained at 25 °C and L14:D10. Each day, aphid infested pieces of grass leaf were sampled randomly from the pots and transferred to the lacewing larvae. Lacewing larvae were fed ad libitum,

thus aphids were never depleted and genotypic effects cannot be interpreted as the result of the available food for the predators.

For each of the five genotypes of *E. repens* we used 15 lacewing larvae. Each lacewing larva was examined daily for development and survival, and the filter paper and the remaining aphids were replaced. Every day, Petri dishes were randomly rearranged in the climate chamber to exclude effects of environmental heterogeneity. As aphid development on genotype 4 was too low to provide lacewing larvae with food, number of replicates for this genotype was reduced to three from day 7. Weight of larvae on the 7th day, weight of the cocoon when pupation had taken place (appearance of a black dot at one end of the cocoon), as well as adult weight after emergence were measured to the nearest 0.1 mg.

Statistical analysis

Data were visually checked for normality of residuals and, if necessary, log-transformed. In all analyses, genotype was treated as a random factor. In the parasitoid experiment, all genotypes were set-up in two replicates per block. Within each block, all replicates were randomized, resulting in a replicated block design including 12 replicates with two independent replicates per genotype and block (Underwood, 1997). The effects of block (cage) and genotype on the number of aphids (including mummies) and number of mummies per plant were analysed using a two-way ANOVA. The influence of grass biomass (dry weight) on aphid numbers and the influence of aphid offspring number on the number of mummies per plant were tested by the inclusion of grass biomass and aphid numbers as covariates. In contrast to simply test the effect on parasitisation rate, this analysis allows for a nonlinear relationship between aphid numbers and parasitism intensity. A two-way ANOVA was applied for the analysis of the effects of genotype and block on mean thorax length and mean pupal development time of hatched parasitoids per plant. This was performed for each sex separately, because males and females were sampled from the same experimental units and sex can therefore not be considered a replicated factor. In the predator experiment, lacewing larvae were fed with aphids from different plants of the respective quackgrass genotypes. This was performed in a randomized way and every lacewing larva received aphids from different individuals of the same genotype during its development. Thus, analyses were performed with the individual lacewing larvae as replicates instead of single individuals of quackgrass. The effect of genotype on larval weight on the 7th day, and the effect of lacewing sex on weight and development time of pupae, as well as weight of adults were tested by a two-way

ANOVA. Non-significant interactions were removed from the analyses. Genotypes were random factors and therefore in ANOVA with a significant genotype effect we calculated the relative variance components (hereafter relative VC) with the expected mean squares method (Quinn & Keough, 2002). Effects of genotype on the mortality of parasitoids during pupal development and mortality of predator larvae as well as sex ratio of hatched parasitoids were tested with a logistic model with binary response variable (including the block factor for the parasitoid experiment). All analyses were performed using STATISTICA 7 (Statsoft, Tulsa, OK, USA).

Results

Parasitoid experiment

Aboveground biomass of *E. repens* differed significantly among genotypes ($F_{4,49} = 9.31$, $P < 0.001$, relative VC = 41%; Figure 1A). Number of aphid offspring differed significantly among genotypes ($F_{4,49} = 7.00$, $P < 0.001$, relative VC = 33%; Figure 1B) and increased with plant biomass (effect of plant biomass as covariate:

$F_{1,48} = 18.52$, $P < 0.001$). Plant biomass may depend on aphid herbivory and therefore the effects of these two variables cannot be disentangled. Nevertheless, including plant biomass as a covariate did not change the general effect of genotype on the number of aphid offspring ($F_{4,48} = 7.77$, $P < 0.001$, relative VC = 39%; Figure 1C). Number of mummies was also affected by plant genotype ($F_{4,50} = 3.88$, $P = 0.008$, relative VC = 19%; Figure 1D) and showed a similar pattern to aphid number (Figure 1B) suggesting that oviposition by parasitoid females increased with aphid density. Number of mummies was positively related to number of aphids. However, after inclusion of aphid number as covariate (effect of aphid number as covariate: $F_{1,49} = 5.10$, $P = 0.04$) genotype had still significant impact on the number of mummies ($F_{4,49} = 2.86$, $P = 0.03$, relative VC = 14%; Figure 1E).

Development time of mummies differed marginally significantly among genotypes for females but not males (females: $F_{4,49} = 2.30$, $P = 0.07$, relative VC = 9.9%; males: $F_{4,28} = 0.47$, $P > 0.3$; Figure 1F). We found no effect of *E. repens* genotypes on thorax length ($P > 0.3$ for both sexes). On average, proportions of female parasitoids were

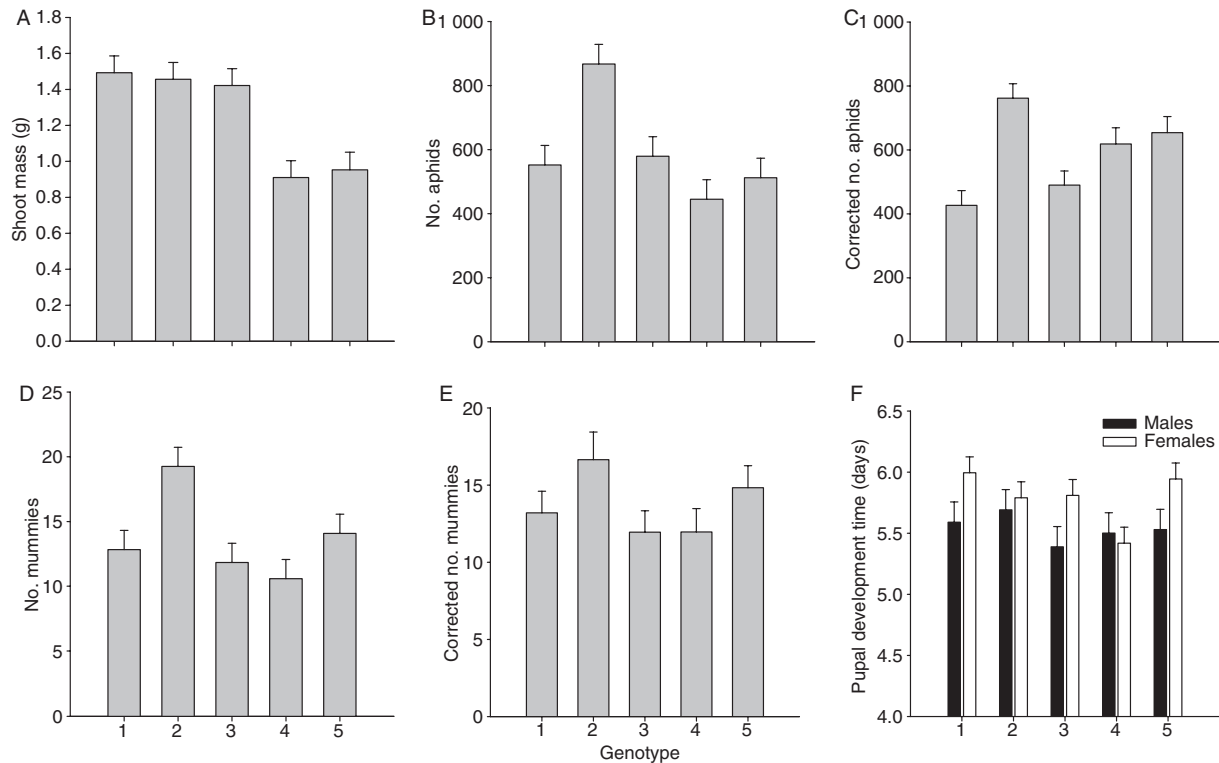


Figure 1 Parasitoid experiment. Influence of *Elytrichia repens* genotype on the mean (+ SE; $n = 12$) (A) shoot dry mass of plants, (B) number of aphids per plant, (C) number of aphids adjusted for plant shoot mass as covariate, (D) number of mummies (parasitized aphids) per plant, (E) number of mummies adjusted for number of aphids as covariate, and (F) pupal development time of *Aphidius colemani* according to sex.

slightly higher than of males, but sex ratios as well as mortality of parasitoids during the pupal development did not vary significantly among genotypes of *E. repens* (logistic regression, in all cases: $P > 0.3$).

Predator experiment

Weight of 7-day-old larvae of *C. carnea* differed significantly among genotypes of *E. repens* ($F_{4,57} = 3.22$, $P = 0.03$, relative VC = 15.2%; Figure 2A). However, there were no significant differences between genotypes in weights of pupae or adults (all $P > 0.1$). Nevertheless, development times differed significantly between predators fed with aphids from different genotypes ($F_{4,30} = 3.41$, $P = 0.02$, relative VC = 26.6%; Figure 2B). There was no effect of sex on development time ($P > 0.3$). Lacewing mortality varied considerably among genotypes (33–86%) but did not differ significantly (logistic regression: $P > 0.03$).

Discussion

Our experiments demonstrated that plant growth, the reproduction of aphids, as well as some performance traits of parasitoids and predators are affected by genotypic variability of *E. repens*. Our results are in line with other studies which showed effects of plant genotype on population growth of aphids (Johnson, 2008; Mooney & Agrawal, 2008). The positive effect of aboveground biomass of grass on aphid numbers may be explained by the general higher availability of resources as well as an increase of feeding sites. However, the effect of genotype remained significant after using biomass as a covariate. Apparently, the different reproduction of aphids on the different genotypes is not only an effect of resource availability but also of resource quality. During our experi-

ment, aphids increased to numbers which are similar to observations in the field (Dixon, 1971) as well as other experiments (Haase et al., 2008) and therefore mirror a realistic situation.

Even if it is sometimes suggested that grasses are mainly defended by silica, the performance of phloem feeders has been shown to not depend on the silica content of the hosts (Massey et al., 2006). Therefore, possible differences in silica contents among genotypes of *E. repens* are unlikely to contribute to the variation of aphid numbers among genotypes during our experiments. *Elytrigia repens* is known to produce allelopathic exudates that affect other plants (Oswald, 1948; Phlak, 1967). Shoots and roots of *E. repens* contain, for instance, cyclic hydroxamic acids (Friebe et al., 1995) which have been shown to decrease the performance of aphids on cereals (Givovich & Niemeyer, 1995; Niemeyer & Perez, 1995). Bezemer et al. (2005) further showed that the concentration of phenolics in the phloem of grasses negatively affects *R. padi*. The differential production of such substances among genotypes may therefore account for differences in aphid densities between host genotypes. Aphid reproduction may be further affected by differences in the nitrogen content in the phloem of the genotypes of *E. repens* (Srivastava, 1987; Dixon, 1998) and potential differences in endophyte infection between quackgrass genotypes (Saikkonen et al., 2000). Clearly, the role of such qualitative traits should be assessed in future studies on the intraspecific variability of bottom-up control in food chains.

The design of our experiment mimics the natural situation with aphid numbers affected by plant and parasitism simultaneously. The effects of plant quality and parasitism on aphid numbers cannot be completely disentangled, but mummy number was low when compared

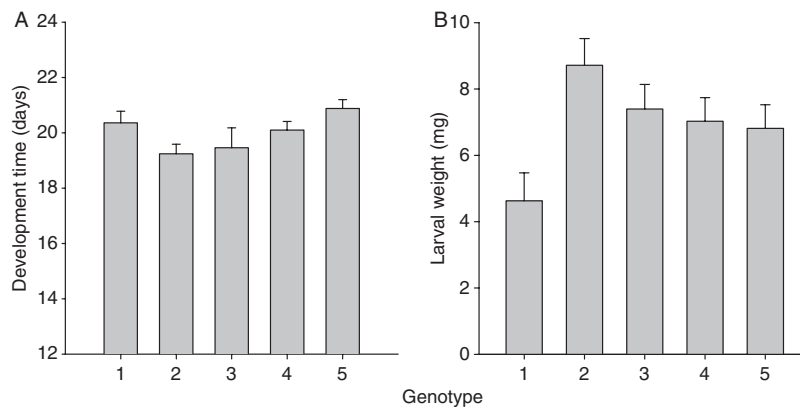


Figure 2 Predator experiment. Influence of *Elytrigia repens* genotype on the mean (+ SE) (A) immature development time (number of replicates because of larval mortality: 10, 11, 13, 14, and 14, for genotypes 1–5, respectively) and (B) larval weight (number of replicates because of larval and pupal mortality: 6, 8, 2, 10, and 10, for genotypes 1–5, respectively) of *Chrysoperla carnea*.

with the total number of aphids per plant and parasitisation rate can therefore be considered as a factor with little impact on our interpretation.

Irrespective of the physiological basis of host suitability for aphids, such differences between plant genotypes have the potential to affect higher trophic levels. Harvey et al. (2003) and Fritz et al. (1997) demonstrated differences in the performance of parasitoids depending on host plant quality. Martos et al. (1992) demonstrated that development time of ladybird larvae decreased when fed with aphids reared on wheat with a high concentration of cyclic hydroxamic acids. In contrast, the parasitoid *Aphidius rhopalosiphii* De Stefani Peres developed slower on such wheat cultivars (Fuentes-Contreras et al., 1998). The change of development time of parasitoids may also reflect changes in the development of the host, as many koinobiont parasitoids do not begin destructive feeding before the host enters its final instar (Harvey et al., 1994). Similar to our study, Fuentes-Contreras et al. (1998) did not find differences in body mass and survival of the parasitoid between the tested cultivars.

A result of our experiments is that the importance of plant genotype, as indicated by the variance components, decreased from herbivores to parasitoids and predators. Herbivorous insects have been shown to be much more limited by the nitrogen content than third-level consumers (Elser et al., 2000; Fagan et al., 2002) what may explain the decrease of the variability of performance traits caused by host genotype along the food chain. From the design of our parasitoid experiment, however, we cannot preclude that this effect may be partly determined by differences between second- and third-level consumers in the ability to make foraging decisions between different genotypes (e.g., because of different dispersal abilities). But this too reflects the situation in natural communities.

In our experiment, the numbers of mummies were positively correlated with the number of aphid offspring, suggesting that ovipositing females of the parasitoid tracked the density of aphids. One reason might be that herbivore-induced release of volatiles may attract herbivore's natural enemies such as parasitic wasps (Stowe et al., 1995; Sabelis et al., 2001). However, we found that a significant amount of variation in the number of mummies among genotypes is not explained by aphid number. Sex ratio of parasitoids may correlate with the quality of host plants because female parasitic wasps are known to have precise control over the sex of their offspring (Godfray et al., 1994). Host quality is known to shift sex allocation towards a female-biased sex ratio in parasitoids developing in hosts on high-quality plants (Charnov, 1982; King, 1987). For female parasitoids, we found genotypic effects on pupal development time. Godfray (1994) showed that development time

is highly correlated to fitness traits in female parasitoids (e.g., number of hosts attacked, longevity). However, we found, no effect of host genotype on body size or sex ratio of parasitoids. Again, this indicates that the effects of genotypes across trophic levels are more complex than suggested by the simple argument that high-quality plants produce 'high-quality' aphids with positive effects on higher trophic levels.

In lacewing larvae, development time differed among genotypes. Although we found significant differences in the weight of larvae, these differences disappeared in the later developmental stages. Larvae may have compensated for low quality of prey by increasing developmental time or feeding rate (Schuler et al., 1996). Legaspi et al. (1996) demonstrated higher survival rates of lacewing larvae feeding on whiteflies which were reared on host plants with higher nutritional quality. In several *Chrysoperla* species (including *C. carnea*), a high nutritional quality of aphid prey has been shown to result in increased larval development, larval survival, pupal weight, adult longevity, and reproduction rates (Chen & Liu, 2001; Liu & Chen, 2001). Some of these performance traits of predators were also affected by plant genotype in our experiment, indicating that genotypic differences influenced predator populations via changed quality or consumption of prey.

The results of our experiments add to the literature which shows that plant genotypes may have significant effects on the performance of herbivorous insects. Furthermore, we also showed that these effects influence higher trophic levels across genotypes originating from natural populations on a small local scale. The influence of plant genotype on predators and parasitoids, however, is weaker than on herbivores. In part, the effect of host genotypes on higher trophic levels is because of some kind of 'mass effect': some genotypes lead to high numbers of aphids that may have attracted parasitoids or caused longer retention time and higher oviposition rates of parasitoids. Even after considering plant biomass or aphid number as a covariate, we found significant differences in the performance of parasitoids between genotypes, although some differences were transient. The design of the predator experiment focussed on plant effects via changed quality of prey and therefore removed density-mediated effects. Therefore, we provide evidence that in addition to density-mediated effects these trait-mediated effects contribute to plant genotypic effects on tri-trophic interactions. Genotypes apparently affect higher trophic levels in both ways and future studies need to focus on the specific mechanisms of trait-mediated effects and the consequences of these effects on fecundity and population dynamics of third-level consumers.

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