

Ecological effects of aphid abundance, genotypic variation, and contemporary evolution on plants

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Abstract Genetic variation and contemporary evolution within populations can shape the strength and nature of species interactions, but the relative importance of these forces compared to other ecological factors is unclear. We conducted a field experiment testing the effects of genotypic variation, abundance, and presence/absence of green peach aphids (*Myzus persicae*) on the growth, leaf nitrogen, and carbon of two plant species (*Brassica napus* and *Solanum nigrum*). Aphid genotype affected *B. napus* but not *S. nigrum* biomass explaining 20 and 7 % of the total variation, respectively. Averaging across both plant species, the presence/absence of aphids had a 1.6× larger effect size (Cohen's *d*) than aphid genotype, and aphid abundance had the strongest negative effects on plant biomass explaining 29 % of the total variation. On *B. napus*, aphid genotypes had different effects on leaf nitrogen depending on their abundance. Aphids did not influence leaf nitrogen in *S. nigrum* nor leaf carbon in either species. We conducted a second experiment in the field to test whether contemporary evolution could affect plant performance. Aphid populations evolved in as little as five generations, but the rate

and direction of this evolution did not consistently vary between plant species. On one host species (*B. napus*), faster evolving populations had greater negative effects on host plant biomass, with aphid evolutionary rate explaining 23 % of the variation in host plant biomass. Together, these results show that genetic variation and evolution in an insect herbivore can play important roles in shaping host plant ecology.

Keywords Community genetics · Eco-evolutionary dynamics · Herbivory · Plant-herbivore · Plant–insect interactions · Rapid evolution

Introduction

Intraspecific genetic variation and contemporary evolution can be important factors shaping the ecology of species interactions (Pimentel 1968; Antonovics 1976; Bolnick et al. 2003; Whitham et al. 2003; Fussmann et al. 2007; Thompson 2013). For example, genetic divergence in feeding and life-history traits of fish can have cascading effects on freshwater communities (Post et al. 2008; Bassar et al. 2010). Similarly, standing genotypic variation in plants affects the performance of individual herbivores (Gould 1983; Fritz and Simms 1992; Underwood and Rausher 2000), and the structure and diversity of entire arthropod communities (Maddox and Root 1987; Wimp et al. 2005; Johnson and Agrawal 2005). When genetic variation in the traits of one species affect ecological interactions with other species, contemporary evolution in a focal species is predicted to alter the performance and abundance of interacting community members (Pimentel 1968; Hairston et al. 2005; Johnson et al. 2009). Although contemporary evolution (evolution over <1–100 years) has been documented in

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a wide diversity of systems (Dyer 1964; Thompson 1998; Bone and Farres 2001; Kinnison and Hendry 2001), few studies have tested the ecological consequences of dynamic evolutionary change on species interactions outside of laboratory microcosms (Rainey and Travisano 1998; Bohannan and Lenski 2000; Yoshida et al. 2007; Schulte et al. 2010; Hersch-Green et al. 2011). In this study, we seek to understand the ecological impacts of genotypic variation and evolution in herbivores on their host plants.

In contrast to the effects of plant genetic variation on herbivores (Maddox and Root 1987; Fritz and Simms 1992; Wimp et al. 2005; Bailey et al. 2009), little is known about whether genetic variation in insect herbivores affects plant physiology and performance (Kant et al. 2008; Utsumi 2011). In one laboratory experiment, genotypic variation in both an aphid (*Sitobion avenae*) and its host plant (*Hordeum vulgare*), interacted with the presence/absence of rhizobacterium to explain more than 40 % of the variance in plant growth (Tetard-Jones et al. 2007). A second laboratory study found that three distinct genotypes of the generalist mite *Tetranychus urticae* feeding on tomato plants differentially induced jasmonic acid-mediated defenses (Kant et al. 2008). These studies suggest that genotypic variation within herbivore populations can influence plant growth and physiology, but the prevalence and importance of these effects are unresolved.

Even less is known about the direct or indirect effects of ongoing evolution in herbivores on the ecology of their host plants. Many studies show that subpopulations of insect herbivores locally adapt to specific species or genotypes of host plants (Brues 1924; Edmunds and Alstad 1978; Van Zandt and Mopper 1998; Tack and Roslin 2010; Farkas et al. 2013), and that such adaptation can occur on short timescales (Gould 1979; Karban 1989; Singer et al. 1993). However, most studies of local adaptation of insect herbivores focused on measuring the performance of the insects, while neglecting to study how variation in herbivores influences physiology, growth, and reproduction of their plant hosts (Mopper 1996). Herbivore evolution can impact plants directly due to changes in the frequency of alleles within herbivore population for genes with important ecological effects on plants. If some herbivore genotypes impose larger negative effects on host plant fitness than others, for example by feeding on fruits rather than leaves, then evolution resulting in increased frequency of those genotypes would have negative impacts on plant fitness. Ongoing herbivore evolution could also impact host plants indirectly by altering herbivore population dynamics (Pimentel 1968; Agashe 2009; Turcotte et al. 2011). For example, genotypes with high fecundity could become more common in growing populations, resulting in even faster population growth than expected with no evolution (Turcotte et al. 2011). Evolution-mediated changes in

population dynamics are expected to impact host plants when the effects of herbivores on plants depend on herbivore population size. Turcotte et al. (2011) conducted laboratory and field experiments with evolving and non-evolving aphid populations. They found that the presence/absence of aphids reduced plant biomass, and although evolution increased aphid populations sizes, evolution itself did not affect host plant biomass. By contrast, rapid adaptation of insect herbivores to different crop varieties is common and can feed back to drastically reduce crop yield (Gould 1991), but the prevalence of this in other systems, and its importance compared to other ecological factors, are unknown.

In this study, we use two field experiments to test the effects of insect herbivore genotype and evolution on host plant performance and physiology. To do this, we used genetically and phenotypically distinct genotypes of the super generalist herbivore green peach aphid (*Myzus persicae*) and two host plants, rapeseed (*Brassica napus*) and black nightshade (*Solanum nigrum*). In our experiments, *M. persicae* only reproduced asexually, which allowed us to manipulate genotype composition of herbivore populations and measure evolution as a change in genotype frequencies over time (Meyer et al. 2006; Turcotte et al. 2011; Agrawal et al. 2012; Zust et al. 2012). Our experiments sought to address the following questions: (1) What is the relative importance of variation in aphid abundance and aphid genotype in affecting the performance and physiology of two plant species? (2) Do aphid populations evolve on their host plants and do different host plants alter the evolutionary rate or trajectories of aphid populations? And (3) does aphid evolution feed back to affect plant growth? Our study provides insight into the importance of genetic variation and contemporary evolution for shaping species interactions.

Materials and methods

Study organisms

Green peach aphid (*Myzus persicae*, Hemiptera: Aphidae) is a phloem-feeding herbivore with a global distribution (Emden et al. 1969). It is an ultrageneralist that feeds on 132 plant families including many agricultural crops (Normark and Johnson 2011). Like many aphid species, *M. persicae* reproduces by cyclical parthenogenesis (i.e., alternating sexual and asexual generations). During the growing season, populations are all female and reproduce asexually. In the fall, females give birth to males followed by a single generation of sexual reproduction. Eggs are typically laid on trees in the genus *Prunus* where they overwinter (Emden et al. 1969). In warmer climates, including the southeastern

United States where this study was conducted, adults can overwinter and forego sexual reproduction completely (Blackman and Eastop 2008). Several studies have documented changes in the frequency of genotypes within populations (i.e. evolution) over weeks to months on individual experimental plants or entire agricultural fields (Vorburger 2006; Turcotte et al. 2011). *Myzus persicae* genotypes are known to contain genetic variation in growth rate (Weber 1986), tolerance to heat and pesticides (Devonshire et al. 1998; Foster et al. 2000; Fenton et al. 2010), resistance to predators and parasitoids (von Burg et al. 2008), and performance on different host plants (Weber 1986; Edwards 2001; Vorburger et al. 2003). In some cases, this variation is attributed to genetic variation in *Buchnera aphidicola*, a vertically transmitted bacterial endosymbiont (von Burg et al. 2008), but since these endosymbionts are vertically transmitted they essentially act as an extended part of the aphids' genome.

Rapeseed (*Brassica napus*: Brassicaceae) is a selfing annual agricultural plant grown worldwide for oil production (Rakow and Woods 1987; Eskin and McDonald 1991). *Brassica* species produce glucosinolates that can negatively affect aphids, including *M. persicae* (Cole 1997). We used the Arriba variety of *B. napus*, which is spring flowering, has low glucosinolate content, and has not been genetically modified using transgenic approaches. Seeds were collected from an open-pollinated field of the same variety so seeds contain limited genetic variation.

Black nightshade (*Solanum nigrum*: Solanaceae) is an annual to perennial herbaceous plant native to Europe. In North America, *S. nigrum* grows in heavily disturbed habitats including agricultural fields, roadsides, and construction sites (Edmonds and Chweya 1997). They predominantly self-fertilize and produce animal dispersed fruits (Edmonds and Chweya 1997). Alkaloids in the leaves make these plants toxic and inedible to many herbivores, although Solanaceae specialists and some generalist arthropods (e.g., *M. persicae*) readily feed on them (Schmidt et al. 2004). The seeds used in the experiment were from a plant collected in Raleigh, NC, that we propagated by selfing in the greenhouse for one generation.

We selected *B. napus* and *S. nigrum* as experimental hosts for several reasons. First, they are distantly related plant species yet both common hosts of *M. persicae* in the wild. Second, we could propagate plants with limited genetic variation, thus we were able to control for this potential source of variation. Finally, they are annuals, which allowed us to measure components of total lifetime fitness. In our experiments we measured plant biomass as a proxy for plant fitness, which was justified by the observation that plant dry biomass was highly correlated with fruit number in *S. americanum* ($r = 0.92$, $df = 7$, $P < 0.001$), but less so in *B. napus* ($r = 0.52$, $df = 13$, $P = 0.047$).

Hereafter, we refer to *B. napus* and *S. nigrum* as *Brassica* and *Solanum*, respectively.

Aphid collections and genotype selection

In summer 2010, we collected 26 clones of *M. persicae* from tobacco fields in eastern North Carolina. We established colonies from single individuals on *Brassica rapa* var. *chinensis* (chinese cabbage) plants. Colonies were grown at room temperature in the laboratory under fluorescent lights set to a 16 h day, 8 h night light cycle. All plants were individually bagged with organza fabric (Bridal Organza, #664-7242; Jo-Ann Fabrics and Crafts, Raleigh, NC, USA) to prevent contamination among colonies. We conducted a preliminary experiment to quantify genotypic variation in growth rate among clones by adding 4 third instar aphids to chinese cabbage seedlings, followed by counting the number of aphids after 7 days; we repeated the experiment twice for each of the 26 clones. We then selected nine aphid clones that spanned the entire range of growth rate (Fig. S1) and genotyped them using microsatellite markers (see “Aphid genotyping” for further details). We selected four genotypes for subsequent experiments that met the following criteria: (1) originated from geographically distinct regions, (2) distinguishable using three polymorphic microsatellite markers (Table S1), and (3) represent the full range in growth rate among the 26 clones (Fig. S1).

Field experiment 1

In this experiment, we tested the relative importance of aphid genotype and aphid abundance on host plant growth and physiological traits in the field. We conducted our field experiments at the Lake Wheeler Field Laboratory of North Carolina State University (35.739N, 78.706W), which has an Appling fine sandy loam soil. We germinated *Brassica* on moist filter paper and *Solanum* by sprinkling seeds on top of wet sand. After germination, we transplanted seedlings to pots (8 cm in diameter) containing 250 cm³ soil and grew them for 12 days in a climate-controlled growth chamber. On 18 May 2011, we transplanted 63 plants of each species into the field. Prior to transplanting, we tilled the field plot and laid down plastic strips to reduce interspecific plant competition. We added 0.1-m-diameter holes every 0.7 m into the strips and transplanted our focal plants in these openings. At this point, *Brassica* and *Solanum* had 2–4 true leaves. Plants were covered in spun polyester bags (Pro 17; Agrofabric, Alpharetta, GA, USA) to exclude non-focal herbivores and predators (Fig. S2). The spatial location of all plant and aphid treatments was fully randomized.

Two days after transplanting, we added third instar aphids to the plants by transferring them with a small

paintbrush. For each plant species and aphid genotype combination, we added aphids to 14 plants at a range of abundances (1, 2, 3, 4, 5, 7, 9, 11, 13, 15, 17, 20, 25, and 32 aphids). We also had seven replicate plants per plant species that did not receive any aphids. We counted aphid population sizes on all plants after 11 days and calculated per capita population growth rate as: $(\ln N_2 - \ln N_1)/(t_2 - t_1)$, where N_1 is the starting population size, N_2 is population size at 11 days, and t is time in days (Agrawal et al. 2004). Twenty-six days after aphids were added, multiple leaves from each plant were harvested and flash-frozen in the field with liquid nitrogen for subsequent elemental analysis. We always sampled the third and fourth fully expanded leaves below the apical meristem to limit phenological and developmental differences. Plants were then cut at the ground, oven-dried, and weighed. We prepared tissue for chemical analyses by first freeze-drying leaves. Next, we ground the tissue into a fine powder by adding 60 mg of tissue to a 2-ml tube with 2.3-mm zirconium beads, followed by shaking at maximum speed in a Powergen High Throughput Homogenizer (Fisher Scientific, USA). Percent carbon and nitrogen were measured at the Ecosystem Analysis Laboratory at University of Nebraska-Lincoln using an HCN elemental combustion analyzer (ECS37 4010 CHNSO Analyzer; Costech Analytical Technologies, Valencia, USA).

Field experiment 2

In this experiment, we tested if host plant shapes aphid evolution and if aphid evolution impacts host plant growth. This experiment was conducted in the same field as Experiment 1 with similar methods. We transplanted 280 plants (140 of each species) into the field in mid-April 2011 when *Brassica* had 4–5 true leaves and *Solanum* had ~8 true leaves. For each plant species, we had six different aphid treatments, which included one monoculture for each of four aphid genotypes, a control with no aphids, and an evolution treatment that included a mixture of all four aphid genotypes. Aphid evolution was not possible in the monoculture treatments because there was only one genotype. Aphid evolution was possible in our evolution treatment because it had four genotypes that could change in frequency over time. For each plant species, there were 20 replicates of each treatment, except the evolution treatment that had 40 replicates. We included more replicates of the evolution treatment to increase our resolution for tracking evolutionary change. We added aphids in late April with each aphid treatment receiving 20 third instar aphids. The aphid evolution treatment received an equal frequency of our four genotypes (5 aphids per genotype). Plants were covered with polyester bags as in Experiment 1. After 4 weeks (~5 generations of population growth), we harvested 15 of the aphid monocultures and control

treatment per species, and 20 of the evolution treatments. At 6 weeks, we harvested the remaining plants (5 of the aphid and control treatments per species, and 20 of the evolution treatments). To determine how genotype frequencies changed after 4 weeks (~5 generations) of population growth, we collected aphids from our evolution treatment by cutting down the plant and beating it over a plastic tray. We then collected >100 haphazardly collected aphids using tweezers into a container with 90 % ethanol. All harvested plants were cut at the ground, oven-dried in paper bags, and weighed.

Aphid genotyping

Before conducting our experiments, we genotyped nine of our clones collected from the field to select our four focal genotypes that had unique haplotypes (Table S1). Using samples collected from Experiment 2, we genotyped up to 16 aphids (range 13–16; 4 plants were excluded from our analyses that had <10 aphids genotyped) that were haphazardly selected from our tube of >100 aphids collected from each of our 40 plants (582 aphids total). We extracted DNA from individual aphids using Chelex[®] 100 (Bio-Rad Laboratories, Hercules, CA, USA) and used PCR to amplify three microsatellite loci identified from previous studies, Mys2, Myz9 (Wilson et al. 2004), and M49 (Sloane et al. 2001). Detailed methods on DNA extraction and PCR conditions are included in the supplementary material. We conducted fragment analysis using a ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) and called alleles for each sample using GeneMarker[®] software (Softgenetics, State College, PA, USA). Based on called alleles, we determined each aphid as being from each of our original four aphid genotypes.

Data analysis

We used analysis of covariance (ANCOVA) to test the effects of aphid treatment on plant traits. For each response variable in Experiment 1, we first fit full models that included aphid genotype, initial starting abundance, two spatial covariates (row and column, which were positions in our grid planting design), and a genotype \times initial abundance interaction as predictor variables. We present results from the best models in each case determined using a forward–backward stepwise selection procedure using the step function in the R package (R Core Team 2013). This function uses model selection to find the combination of predictor variables that leads to the lowest AIC. We calculated the amount of variance explained by genotype as: $(\text{sums-of-squares for the genotype factor})/(\text{total sums-of-squares}) \times 100$. Models were fit with Type III sums of squares using the Anova function in the

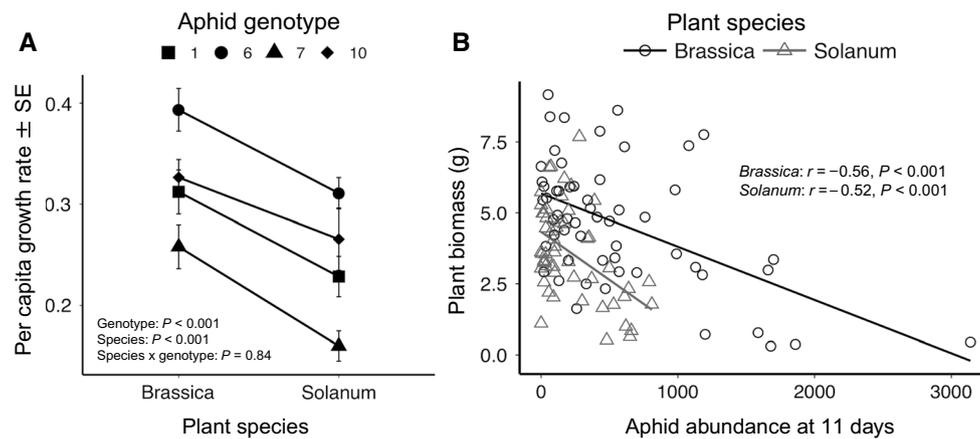


Fig. 1 Differences among aphid genotypes and impacts of aphid abundance on plant biomass. **a** Population growth rates of four aphid genotypes on two host plants, *Brassica* and *Solanum*. Aphid genotypes differ in growth rate, and all aphid genotypes grew slower on *Solanum* than *Brassica*. There is no aphid genotype \times plant species

interaction. **b** The effects of aphid abundance at 11 days on final dried plant biomass for both *Brassica* and *Solanum*. Increasing aphid abundance decreased plant biomass on both species. Linear regression lines are added to show trends

car package (Fox and Weisberg 2011). We used Pearson's correlations to test the relationships between aphid abundance and plant biomass and calculated variance explained as $r^2 \times 100$. We compared the relative importance of aphid genotype to the presence/absence of aphids by calculating Cohen's d standardized effect size among genotype treatment means and means for plants with and without aphids, respectively (Cohen 1988). Cohen's d is the difference in means among levels of a treatment divided by pooled standard deviation. For the genotype treatments, we calculated this difference as the mean pairwise difference among genotype means. For all calculations, we used residual plant biomass after accounting for covariates.

For Experiment 2, we used the same ANCOVA approach as above to test the effects of aphid treatment on plant biomass. However, we did not have an initial starting abundance covariate and we included a temporal blocking factor according to plants that were harvested after 4 or 6 weeks. On the evolution treatment, we calculated the relative frequencies of each aphid genotype on each plant such that the frequencies of the four genotypes added to 1. We determined if evolution occurred (i.e. changes in genotype frequency) by calculating the multivariate Euclidian distance of the final population frequencies from the starting frequencies of 0.25. This gave us a single value of the rate of evolution on each plant; values range from 0 (i.e., no deviation from equal genotype frequencies) to 1 (i.e., all aphids were of one genotype). We then calculated 95 % confidence intervals around these values and tested if intervals among treatments overlap. To test the effects of plant species on aphid evolution, we used multivariate analysis of variance using the manova function in R. In this model,

the frequencies of all the genotypes were the multivariate response variables, and plant species (either *Brassica* or *Solanum*) was the predictor. We tested if the mixture treatments were different from the single genotype treatments by fitting an ANCOVA with the same covariates as above and a two-level factor indicating if the plant had a single aphid genotype treatment (aphid genotype 1, 6, 7, 10) or a mix treatment. Finally, to test the effects of evolution on plants, we correlated the rate of aphid evolution against plant biomass. All analyses were done in R v.3.0.2 (R Core Team 2013).

Results

Experiment 1

Aphid populations grew rapidly in the field. After 11 days, the average population size was 400 aphids per plant (range 7–3000). Aphid genotypes varied in per capita growth rate by 1.7 \times , between the slowest and fastest growing genotypes ($F_{3,101} = 16.7, P < 0.001$). Although aphids grew 25 % slower on *Solanum* than *Brassica* ($F_{1,101} = 30.8, P < 0.001$; Fig. 1), the rank order of genotype growth rates was the same on both species (aphid genotype \times plant species interaction: $F_{3,98} = 0.27, P = 0.84$; Fig. 1).

Aphids had strong negative effects on plant growth. Aphid abundance at 11 days was negatively correlated with plant biomass on both *Solanum* (Pearson's correlation, $r = -0.52, df = 61, P < 0.001$; Fig. 1a) and *Brassica* ($r = -0.56, df = 61, P < 0.001$; Fig. 1b). This effect of aphid abundance explained 27 and 31 % variation in plant biomass on *Solanum* and *Brassica*, respectively.

Table 1 ANCOVA tables for the effects of aphid genotype and abundance on the biomass, leaf carbon and nitrogen of both *Brassica napus* and *Solanum nigrum* in Experiment 1

Factor	Biomass				% Carbon				% Nitrogen			
	SS	df	F	P	SS	df	F	P	SS	df	F	P
<i>Brassica</i>												
Genotype	49.62	3	6.96	<0.001	8.21	3	1.42	0.25	1.70	3	2.27	0.09
Abundance	48.28	1	20.33	<0.001	0.99	1	0.51	0.48	0.37	1	1.47	0.23
G × abd					12.88	3	2.22	0.10	7.34	3	9.83	<0.001
Row	11.75	1	4.95	0.03					12.40	1	49.80	<0.001
Column	24.88	1	10.48	0.002					0.42	1	1.68	0.20
Residuals	116.38	49			86.82	45			10.70	43		
<i>Solanum</i>												
Genotype	10.80	3	1.85	0.15	0.43	3	0.12	0.95	0.70	3	0.96	0.42
Abundance	13.82	1	7.11	0.01								
G × abd	18.70	3	3.21	0.03								
Row	10.62	1	5.46	0.02					17.86	1	73.31	<0.001
Column												
Residuals	91.36	47			64.17	51			12.18	50		

Abundance of aphids at the start of the experiment and two spatial covariates (*row* and *column*) are included as covariates. Here, we present the best model determined by stepwise selection using AIC values. Aphid genotype only had clear effects on *Brassica* biomass while aphid abundance shaped biomass in both plant species. Aphid genotype and abundance interacted to shape nitrogen levels on *Brassica* but not on *Solanum*. Bold type indicates significance at $p < 0.05$

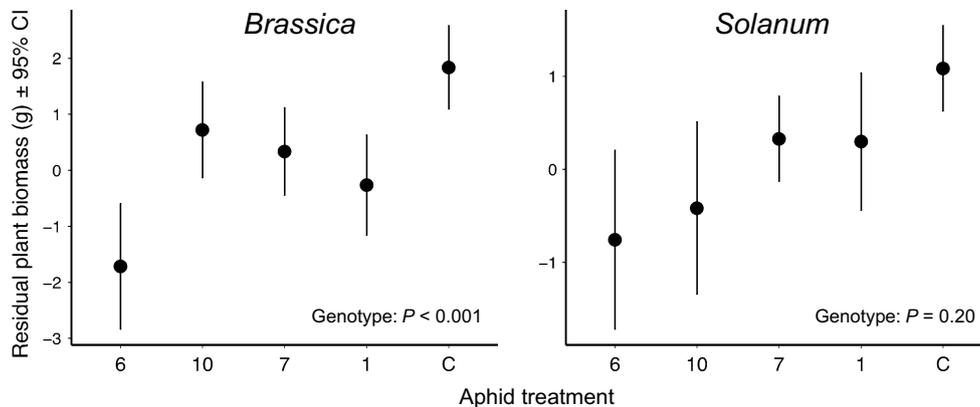


Fig. 2 The effects of aphid genotype and control with no aphids (C) on the biomass of both *Brassica* and *Solanum* in Experiment 1. y-axes represent residuals of models predicting plant biomass fit with covariates but not aphid treatments. Circles show means and error

bars 95 % confidence intervals. Tukey HSD multiple comparison tests show that aphid genotype 6 is significantly ($P < 0.05$) different than the control on *Solanum* and significantly different from all other treatments in *Brassica*

Aphid genotype had variable effects on plant biomass. On *Brassica*, aphid genotype was a significant predictor of plant biomass (Table 1) and explained 20 % of the variation in our model. This effect of aphid genotype was largely driven by genotype 6, which reduced plant biomass more than the other three genotypes (Fig. 2). The effects of aphid genotype on *Brassica* biomass was not significant when aphid abundance at 11 days was included in the model ($F_{3,49} = 18.2$, $P = 0.08$), suggesting that the genotypic

effects were driven primarily through effects on aphid population growth rate. Aphid genotype did not significantly affect *Solanum* biomass (Table 1) and only explained 7 % of the variation in our models. Overall, the presence/absence of aphids had a 1.6× larger effect size (Cohen's d) on plant biomass than did aphid genotype treatment (Fig. 3).

The effects of aphid genotype on plant nitrogen depended on the plant species and initial aphid

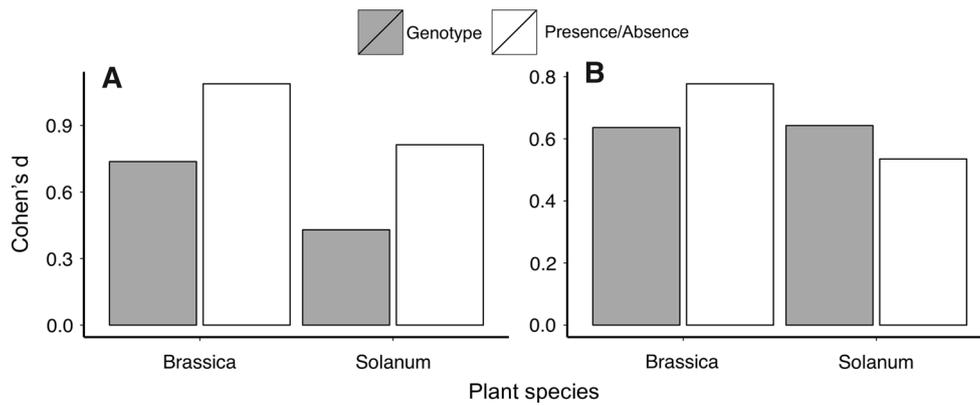


Fig. 3 Effect size of aphid manipulations on plant biomass from Experiment 1 (a) and Experiment 2 (b). The y-axis shows Cohen's *d* effect sizes in standard deviation units of aphid treatments on plant biomass (note: the scale differs between a and b). 'Genotype' effect sizes represent the mean differences among our four solo genotype treatments and the 'presence/absence' effect represents the differ-

ences between our no-aphid controls and all other treatments with aphids added. The presence/absence of aphids has larger effects on plant biomass in Experiment 1, while aphid genotype and the presence/absence of aphids has similar effects on plant biomass in Experiment 2

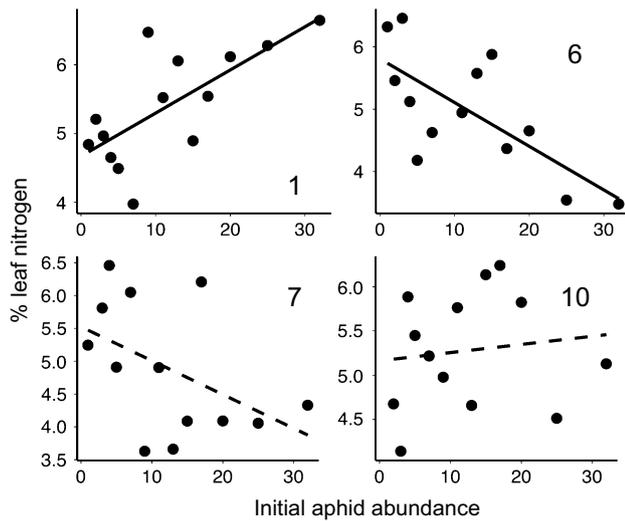


Fig. 4 Interactive effects of aphid genotype and initial aphid abundance on *Brassica* percent leaf nitrogen content. Each panel shows a different aphid genotype (1, 6, 7, 10). Solid fit lines are significant relationships (genotype 1, $P = 0.02$; genotype 6, $P = 0.03$) and dashed lines are not significant ($P > 0.4$)

abundance. On *Brassica*, we observed a significant aphid genotype \times initial abundance interaction (Table 1; Fig. 4). Aphid genotype 6 showed a negative relationship between initial aphid abundance and percent leaf N ($t_{11} = -3.30$, $r = -0.70$, $P = 0.029$, with Bonferroni correction), while aphid genotype 1 showed a positive relationship ($t_{12} = 3.51$, $r = -0.71$, $P = 0.017$, with Bonferroni correction); the effects of the other two genotypes on leaf nitrogen did not vary with initial abundance (Fig. 4). Aphid genotype did not affect leaf nitrogen in

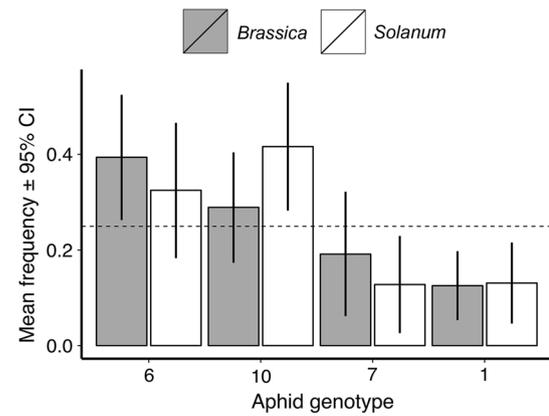


Fig. 5 Changes in aphid genotype frequency on *Brassica* and *Solanum*. Bars show the frequencies of four aphid genotypes inferred from identifying the clonal identity of 16 aphids per plant. The dotted line shows the initial starting frequency of all aphids at equal abundance. Aphid populations evolved (i.e., genotype frequencies deviated from initial starting frequencies) on *Brassica* (Euclidean distance = 0.41, 0.95 % CI 0.34–0.48) and *Solanum* (Euclidean distance = 0.39, 95 % CI 0.32–0.47), but these evolutionary trajectories were not affected by plant species (MANOVA, approximate $F_{3,32} = 0.75$, $P = 0.52$)

Solanum and leaf carbon was unaffected in both species (Table 1).

Experiment 2

Aphid populations evolved in the ~ 5 generations of the experiment and rates of evolution were similar on both *Solanum* (Euclidean distance = 0.39, 95 % CI 0.32–0.47) and *Brassica* (Euclidean distance = 0.41, 0.95 % CI 0.34–0.48). As expected, faster reproducing genotypes (6

Table 2 Effects of aphid genotypes on *Brassica* and *Solanum* biomass in Experiment 2

Factor	<i>Brassica</i>				<i>Solanum</i>			
	SS	df	F	P	SS	df	F	P
Genotype	7252.42	4	5.20	<0.001	6337.25	4	4.11	0.004
Column	8256.03	1	23.68	<0.001	5030.13	1	13.05	<0.001
Row	2359.27	1	6.77	0.01	21.66	1	0.06	0.81
Harvest	5324.68	1	15.27	<0.001	9411.28	1	24.43	<0.001
Residuals	38,348.68	110			43,924.59	114		

Column and row are spatial covariates and Harvest is a temporal covariate. Aphid genotype treatment had highly significant effects on plant biomass in both species. Bold type indicates significance at $P < 0.01$

Fig. 6 The effects of aphid genotype (genotypes: 1, 6, 7, 10), evolution treatment with all genotypes, and controls with no aphids (C) on the biomass of both *Brassica* and *Solanum*. These data are from experiment 2. y-Axes represent residuals of models predicting plant biomass fit with covariates but not aphid treatments. See Table S1 for results of multiple comparisons tests on these data. Circles show means and error bars 95 % confidence intervals

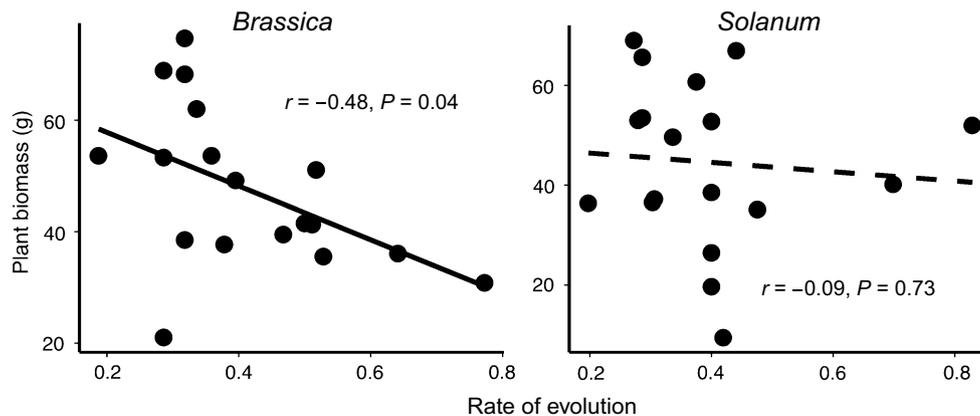
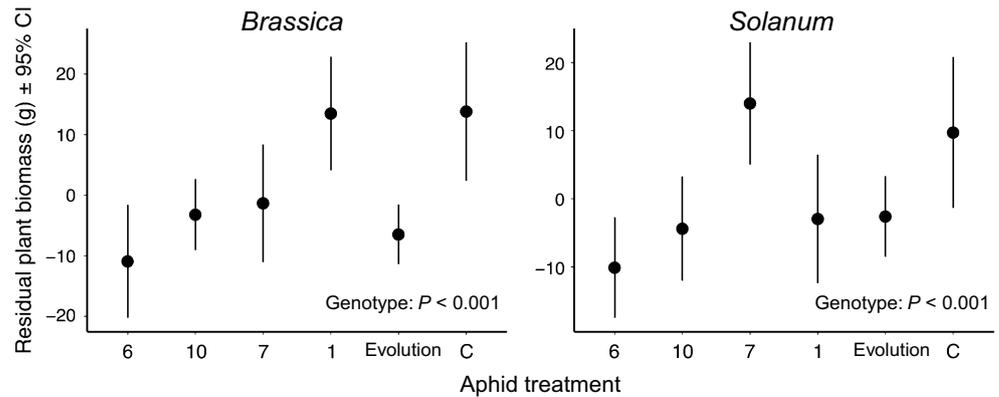


Fig. 7 Correlation between rate of aphid evolution and the biomass of the host plants after 4 weeks in Experiment 2. Rate of evolution is measured as the Euclidian distance between initial genotype frequencies and the final population genotype frequencies. Final geno-

type frequencies were inferred by genotyping 16 aphids per plant. On *Brassica*, plants with faster evolving aphid populations have reduced plant biomass but there is no correlation on *Solanum*. Linear regression lines are added to show trends

and 10) became more common and slower reproducing genotypes (1 and 7) became less common (Fig. 5). Evolutionary trajectory was consistent across both plant species (MANOVA, approximate $F_{3,32} = 0.75$, $P = 0.52$; Fig. 5), and thus aphid populations did not genetically diverge among host plant species.

Our aphid genotype manipulations significantly affected host plant biomass in both *Solanum* and *Brassica* (Table 2; Fig. 6). On both plant species, aphid genotypes 6 and 10 had the largest negative effects on plant biomass (Fig. 6; Table S1). On *Brassica*, our genetically mixed evolution treatment reduced plant biomass more than aphid treatment

containing a monoculture of genotype 1, while the evolution treatment was not significantly different from the other aphid genotype monoculture treatments (Fig. 6; Table S1). Overall, the presence/absence of aphids and aphid genotype treatments had similar effects sizes on plant biomass (Fig. 3).

We found that aphid evolution negatively affected host plant growth on one of the two plant species. On *Brassica*, we found a negative correlation between the rate of evolution and plant biomass ($r = -0.48$, $df = 16$, $P = 0.04$; Fig. 7), while there was no such effect on *Solanum* ($r = -0.09$, $df = 16$, $P = 0.73$; Fig. 7). Overall, the evolution treatment had similar effects on plant biomass as the mean effect of the four single genotype treatments on *Brassica* ($F_{1,113} = 2.79$, $P = 0.098$) and *Solanum* ($F_{1,117} = 0.06$, $P = 0.81$).

Discussion

We used two field experiments to test the ecological consequences of genetic variation and contemporary evolution in a rapidly reproducing insect herbivore. Our results support three general conclusions about the interactions between ecology and evolution in this plant–aphid system. Firstly, aphid genotypes showed large variation in their population growth rates that often resulted in differential impacts on host plant growth. These genotype effects were, in some cases, comparable to the effects of the presence/absence of aphids, but aphid genotype still explained less of the total variance in plant growth than aphid abundance. Secondly, aphid populations evolved over the course of five generations, but host plant species did not affect the rate or trajectory of evolution. Thirdly, the ecological impacts of aphid evolution on plant growth varied between host plant species, where the fastest evolving aphid populations also had the largest negative impact on plant growth of *Brassica*. Evolutionary rate explained 23 % of the variation in plant biomass, which is comparable to the variance explained by aphid genotype and aphid abundance. Together, these results show that genetic variation and contemporary evolutionary dynamics in an insect herbivore are important predictors of plant growth and physiology, and ignoring these factors could limit our understanding of the evolutionary ecology of plant–herbivore interactions.

Relative importance of herbivore genotypic variation on host plants

Herbivores often have negative consequences on plant growth and reproduction (Hawkes and Sullivan 2001; Maron and Crone 2006), but the relative ecological importance of herbivore genetic variation compared to the

presence/absence of herbivores or variation in herbivore abundance is unknown. This represents a notable gap in our understanding of the evolutionary ecology of plant–herbivore interactions because ecologists typically assume that genotypic variation is of minimal ecological importance compared to ecological factors such as community composition or species abundance (Hersch-Green et al. 2011). This assumption is problematic because there is now considerable evidence showing genetic variation within and among populations of arthropod herbivores for numerous phenotypic traits (Brues 1924; Gould 1983; Mopper 1996), especially in agricultural systems (Pathak and Painter 1959; Gould 1983; Weber 1986). To elucidate the ecological importance of genetic variation in herbivores, we compared the effects of aphid genotype to that of the presence/absence of herbivores and herbivore abundance. We found that the presence/absence of aphids had larger effects on plant biomass than aphid genotype in Experiment 1, while there was no clear difference between these factors in Experiment 2 (Fig. 4). Aphid abundance, however, explained more of the total variance in plant growth than aphid genotype. In our models, aphid abundance explained >25 % of variation in plant biomass averaged across both host plant species, whereas aphid genotype explained 20 % in *Brassica* and 7 % in *Solanum*. These effects of aphid genotype on plants appear to be mainly caused by genotypic variation in fecundity, because aphid genotype was not a significant predictor of plant biomass when aphid abundance at 11 days was included as a covariate. Together, these results suggest that which aphid genotype lands on a plant can be as important as the presence/absence of aphids, although in both cases these effects are mediated by variation in herbivore abundance.

We saw variable effects of aphid abundance and genotype on leaf nitrogen. Herbivory often induces changes in plant physiology which can be dependent on herbivore species (Karban and Baldwin 1997; Walling 2000; Kessler and Baldwin 2002; Viswanathan et al. 2005) and even herbivore genotype (Kant et al. 2008). For example, proteins in aphid saliva can cause induced changes in plant physiology and may even manipulate nitrogen levels to benefit insects (Miles 2007; Rodriguez-Saona et al. 2010). We found some evidence that aphid genotypes differ in their impacts on plant nitrogen, but these effects were dependent on herbivore abundance (Fig. 4). While it is not clear if aphids manipulated plant nitrogen in our experiments, our results do suggest that such effects of aphids on plant physiology might be dependent on aphid abundance and genotype.

Causes of *Myzus persicae* contemporary evolution

Variation within or among plant species is often an important agent of selection on arthropod herbivores. Local

adaptation of herbivores to plant species, genotypes, or even individuals appears to be widespread (Via 1990; Mopper 1996; Zandt and Mopper 1998; Nasil et al. 2002; Tack and Roslin 2010). Furthermore, a number of controlled selection experiments demonstrate contemporary adaptation to host plant species or genotypes (Painter 1931; Gould 1979; Wasserman and Futuyma 1981; Pathak and Heinrichs 1982; Fry 1990; Agrawal 2000; Meihls et al. 2008; Soria-Carrasco et al. 2014). However, adaptation to host plants is not universal as many studies also find no evidence of local adaptation (Gould 1983; Strauss 1997; Van Zandt and Mopper 1998; Tack and Roslin 2010). *Myzus persicae* often shows genetic variation in performance on different host plant species (Weber 1986; Edwards 2001; Vorburger et al. 2003), while Gould (1983) reported on a study showing no aphid genotype \times plant genotype interactions when testing performance of multiple *M. persicae* populations on 61 wild potato genotypes. We found that populations evolved over the course of our experiment, with the two most rapidly reproducing genotypes increasing in frequency. Overall, it appears that populations did adapt to host plant and/or environmental conditions. Our two host plants varied in resistance to *M. persicae*, but we saw no aphid genotype \times plant species interaction and no genetic variation within aphids for host plant use. There were also no differences in evolutionary rates or trajectories between plant species and thus no signature of local adaptation to individual plant species.

Ecological consequences of herbivore contemporary evolution

When genotypes vary in their ecological effects on interacting species, and evolution occurs on contemporary time-scales, ongoing evolutionary change is expected to impact ecological processes (Hairston et al. 2005; Fussmann et al. 2007; Johnson et al. 2009). Agricultural plant–herbivore systems represent some of the best examples of contemporary evolution feeding back to affect ecological interactions. For example, the introduction of transgenic crops producing *Bacillus thuringiensis* (Bt) toxins resulted in drastic reductions in herbivory and increased crop yield. However, several species subsequently evolved resistance to Bt toxins and these evolutionary changes can result in increased damage on crop plants and reduced yield (Tabashnik et al. 2009). These evolutionary changes can happen very quickly. A selection experiment with western corn rootworm (*Diabrotica virgifera virgifera*, Coleoptera: Chrysomelidae) resulted in the evolution of 22-fold increase in Bt resistance after just three generations (Meihls et al. 2008). Herbivore adaptation to conventional crop varieties is also common. For example, the hessian fly (*Mayetiola destructor*, Diptera: Cecidomyiidae) has

repeatedly evolved the ability to feed on resistant varieties of wheat in less than 10 years (Foster et al. 1991; Rausher 2001). It is not clear, however, if these ecological impacts of herbivore evolution are unique to agricultural systems, where plant genotypes produced by artificial selection likely impose stronger selection on herbivores than in natural systems.

We found that contemporary evolution in herbivores can be an important factor shaping plant growth. We tested the ecological effect of aphid evolution in our system in two ways: (1) by comparing the effects of evolving populations on host plant biomass to non-evolving populations; and (2) by correlating the observed rate of aphid evolution on each plant with the plant's final biomass. The first test did not provide evidence for ecological effects of contemporary evolution because evolving populations had similar effects on plant biomass as three of the four single aphid genotype treatments. This is a somewhat crude test, however, because the ecological effects of evolution would only be detected if outcomes of evolving populations fall outside the range seen among the monoculture treatments, which they do not. In our second test, we found a significant negative correlation between aphid evolutionary rate and *Brassica* biomass (Fig. 7). Although we cannot definitively determine cause and effect from this relationship, it suggests that faster evolving populations have larger negative impacts on plant growth. Because the effects of aphids on plants are mainly a function of aphid abundance, it is likely that faster evolving populations have larger population sizes. This could be because evolution actually results in faster population growth, as seen in another experiment with *M. persicae* (Turcotte et al. 2011). Alternatively, external factors could cause some populations to reproduce more quickly than others, and this greater number of generations resulting in greater change in genotype frequency (i.e., faster rate of evolution). Regardless of the exact mechanism, our results support the general hypothesis that faster evolving parasite populations will have larger negative impacts on their hosts.

Conclusions

Theoretical and empirical evidence suggests that ongoing evolutionary change can be important in shaping species interactions, communities, and ecosystems (Abrams 2000; Hairston et al. 2005; Fussmann et al. 2007; Post and Palkovacs 2009). Plant–herbivore interactions seem likely to be shaped by contemporary evolution given the known ecological importance of genetic variation in plant–herbivore interactions (Gould 1983; Fritz and Simms 1992; Underwood and Rausher 2000; Johnson and Agrawal 2005) and the propensity for arthropod herbivore populations

to rapidly evolve (Gould 1979; Vorburger 2006; Loxdale 2010; Carrière et al. 2010). Here, we show that effects of different genotypes of a rapidly reproducing herbivore on host plant growth can be as large as the effects of herbivore presence/absence. We also document evolutionary change over just a few generations, and find evidence that faster evolving populations have larger negative effects on host plant growth. These results together highlight the potential importance of intraspecific variation and contemporary evolution in shaping the ecology of plant–herbivore interactions. In some cases, ecologists will need to consider evolutionary processes to understand the strength and dynamics of species interactions. This is particularly noteworthy in the study of plant–herbivore interactions where researchers often study variation in plants but ignore variation and evolution in herbivores.

Author contribution statement N.E.T. and M.T.J.J. developed ideas and designed the field experiments; N.E.T. conducted experiments and collected data with help from M.T.J.J.; N.E.T. analyzed data and wrote the first draft of the paper; N.E.T. and M.T.J.J. edited the paper.

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