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BOTTOM-UP EFFECTS OF PLANT GENOTYPE ON APHIDS, ANTS, AND PREDATORS

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Abstract. Theory predicts that bottom-up ecological forces can affect community dynamics, but whether this extends to the effects of heritable plant variation on tritrophic communities is poorly understood. In a field experiment, I contrasted the effects of plant genotype (28 genotypes; 1064 plants), aphid density, and the presence/absence of mutualistic ants in affecting the per capita population growth of a specialist aphid herbivore, as well as the effects of plant genotype on the third trophic level. Plant genotype strongly affected aphid population growth rate, explaining 29% of the total variation in growth rate, whereas aphid density and ant–aphid interactions explained substantially less variation (<2%) in aphid population growth rate. Plant genotype also had direct and indirect effects on the third trophic level, affecting the abundance of aphid-tending ants and the richness of predators. Multiple regression identified several heritable plant traits that explained 49% of the variation in aphid growth rate and 30% of the variation in ant abundance among plant genotypes. These bottom-up effects of plant genotype on tritrophic interactions were independent of the effects of either initial aphid density or the presence/absence of mutualistic ants. This study shows that plant genotype can be one of the most important ecological factors shaping tritrophic communities.

Key words: *ant–aphid mutualism;* Aphis oestlundi; *community genetics; extended phenotype; genetic variation;* Oenothera biennis; *plant–insect ecology; top-down; tritrophic interactions; trophic cascade.*

INTRODUCTION

Population dynamics are governed by bottom-up and top-down processes in multitrophic communities (Nicholson 1933, Elton and Nicholson 1942, Hairston et al. 1960, Hunter and Price 1992). For arthropods, intraspecific variation in plant quality is hypothesized to be a key factor affecting the growth and regulation of populations (Painter 1951, Haukioja 1980, Rhoades 1983, White 1984, Underwood and Rausher 2000). In particular, genetic differences among plants in their plant traits can have direct and indirect effects on herbivore populations (Karban 1987, Underwood and Rausher 2000, 2002, McIntyre and Whitham 2003, Fritz and Hochwender 2005, Johnson and Agrawal 2007), predators (Price et al. 1980, Weis and Abrahamson 1986, Fritz 1995, Stiling and Rossi 1996, Fritz and Hochwender 2005, Bailey et al. 2006), and the mutualists of herbivores (Wimp and Whitham 2001). Such bottom-up effects of plant genotype may interact with top-down predation and mutualistic interactions to influence herbivore population dynamics (Hare 2002), but the relative importance of these factors has not been investigated. Here I examine the importance of plant genotype, aphid density, and mutualistic interactions in affecting the population dynamics of a specialist herbivore, as well as the abundance and species richness at the third trophic level.

Genetic variation in plant traits frequently affects the preference and performance of individual herbivores, which has led to the hypothesis that genetic variation in resource quality can influence herbivore population dynamics (Karban 1992). Early evidence for this hypothesis came from agricultural systems, in which differential resistance among crop varieties affected the fecundity and short-term population growth of herbivores (Painter 1951, Webster et al. 1991, Underwood and Rausher 2000). For example, different soybean genotypes that varied in constitutive and induced resistance affected per capita reproduction of Mexican bean beetles, which was predicted to have long-term consequences for population dynamics (Underwood and Rausher 2000, 2002). Recent studies also provide evidence that genetic variation in natural plant populations can influence the size and growth of herbivore populations (Karban 1987, McIntyre and Whitham 2003, Johnson and Agrawal 2007, Underwood 2007).

In addition to the bottom-up effects of plant genotype, the top-down influence of predators and mutualists can affect herbivore population dynamics. Predators impose density-dependent mortality when increased herbivore abundance results in greater predation (Varley and Gradwell 1970, Hassell 1978, Murdoch et al. 2005). Some predators also serve as facultative mutualists to herbivores, such as ants that protect

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Lycaenid caterpillars and Hemiptera from predators in exchange for honeydew (Pierce et al. 2002, Stadler and Dixon 2005). Mutualistic ants may alter density-dependent predation when they themselves recruit to herbivores in a density-dependent manner (Breton and Addicott 1992*a*). Of course, the top-down effects of predators and mutualists may not be independent of the bottom-up effects of plant quality. Genetic variation in plant traits may directly affect predators and mutualists (Breton and Addicott 1992*b*, Rudgers 2004) or indirectly affect the third trophic level via direct effects on herbivores (Bailey et al. 2006). Disentangling this complexity will help illuminate the factors that govern species interactions across multiple trophic levels.

In this study, I conducted a field experiment to understand how bottom-up and top-down ecological forces affect interactions between a native plant (*Oenothera biennis* L.), a specialist aphid herbivore (*Aphis oestlundi*), and the mutualists and predators of the herbivore (see Appendix A). My objectives were twofold. First, I sought to understand the relative importance of plant genotype of *O. biennis*, initial aphid density, and ant mutualists in affecting the population dynamics of the specialist aphid herbivore. Second, I investigated whether the bottom-up effects of plant genotype directly and indirectly influenced the abundance of mutualistic ants and arthropod predators. Given the strong effects of plant genotype on herbivore populations and the third trophic level, I also examined whether genetic variation in specific plant traits predicted variation in aphid population growth rate, ant abundance, and predator richness.

Materials and Methods

Study system

Common evening primrose (*Oenothera biennis* L., Onagraceae) is a native, facultative, biennial plant that commonly occurs in open habitats. Individual plants produce copious clonally related seeds, which is a function of the unique genetic system possessed by *O. biennis*, permanent translocation heterozygosity (Cleland 1972). This genetic system makes it possible to grow numerous replicate plants from seed of single clonal genotypes. Populations of *O. biennis* exhibit substantial quantitative and qualitative genetic variation for many morphological, phenological, and chemical traits (Johnson and Agrawal 2005, Johnson 2007; Appendix B).

The aphid *Aphis oestlundi* (Gillette) is an herbivore specific to *Oenothera* spp. Non-winged (most abundant) and winged individuals are both produced, and reproduction is viviparous and parthenogenetic. Populations can rapidly increase and outbreak on individual plants as newborn nymphs can reproduce within seven days. Detailed observations of >1500 plants in the two years prior to this experiment showed that aphid populations ranged from 0 to 438 individuals per plant, though populations were typically small (<10 individuals) (*personal observations*). *Aphis oestlundi* commonly feeds and aggregates on senescing leaves and apical growth, and its entire life cycle can occur on *O. biennis*; its overwintering behavior is unknown. During the experiment, six ant species naturally tended and collected honeydew from *A. oestlundi*. In order of decreasing relative abundance, these species were: *Formica* sp., *Myrmica* sp., *Lasius* sp., *Leptothorax* sp., *Tapinoma* sp., and *Crematogaster lineolata* (Say).

A diversity of generalist predators preyed on *A. oestlundi* during the experiment. Spiders and syrphid larvae were the most frequent predators. Coccinellids (larvae and adults), Chrysopids, Heteroptera (e.g., Geocoridae), Coleoptera (e.g., Staphylinidae), and predatory mites also occurred. Hymenopteran parasitoids were rare.

Experimental design

I conducted this research at the University of Toronto's Koffler Scientific Reserve at Jokers Hill in Ontario, Canada. To contrast the effects of plant genotype, aphid density, and mutualistic ants on aphid populations, I manipulated these factors in a fully factorial field experiment.

Manipulation of plant genotype.—I used 28 clonal genetic families (hereafter genotypes) of *O. biennis*, collected as seed during 2002 and 2003 from plants within 12 km of Jokers Hill. I germinated 28–40 seeds from each genotype (1064 plants) simultaneously on Petri dishes in mid-February and transplanted seedlings into 500-mL pots containing soil (Promix General Purpose BX soil; Premier Horticulture, Dorval, Quebec, Canada) with 0.25-g slow-release fertilizer pellets added to the soil surface (13:13:13, N:P:K; Vicksburg Chemical, Vicksburg, Mississippi, USA). Plants grew in a rooftop greenhouse for 11 weeks at 25°C supplemented with 400-W sodium lamps set to a 14:10 h (day : night) light cycle. I moved plants to Jokers Hill for hardening in early May and subsequently removed plants from their pots and transplanted them into the ground within an old field. I left the surrounding vegetation intact. All plants were completely randomized into a rectangular grid pattern with 1-m spacing between rows and columns. I further subdivided the common garden into four equal-sized spatial blocks to account for environmental variation; all genotypes were replicated in each block. I bagged plants with spun polyester to prevent herbivory prior to applying the experimental treatments. Most plants remained in the rosette stage throughout the experiment, although a minority started to bolt by the end of the experiment.

Manipulation of specialist aphid herbivore.—In early spring 2004, I started a colony of *A. oestlundi* from several aphids collected from a single leaf of *O. biennis* at Jokers Hill. Given the reproductive biology of *Aphis*, the aphid colony was likely started from a single clonal genotype. In mid-July, I removed the bags from all plants and randomly assigned each plant to one of five

initial aphid densities (0, 2, 5, 8, and 11 aphids/plant), with approximately equal replication per plant genotype. This range of densities was chosen to reflect the number of aphids observed to naturally occur on wild plants early in summer when aphid populations are beginning to establish and grow on plants (*personal observations*). Plants in the no-aphid treatment served as controls to measure plant traits and to assess whether aphids dispersed among plants. Aphids moved very little among plants, and I terminated the experiment when the first aphids appeared on control plants. The final density of aphids on experimental plants was comparable to that found on nearby naturally occurring *O. biennis* plants. Aphid populations decline in September and October (*personal observations*) and so my observations reflected the most active growth period for *A. oestlundi*.

Manipulation of ants.—I manipulated the presence/absence of ants using aluminum cylinders (25 cm diameter, 15 cm [short cylinders] or 20 cm [tall cylinders] high) placed around each plant. To exclude ants, I sunk the tall cylinders ~3 cm into the ground and covered the rim with Tanglefoot, a spreadable sticky paste that ensnares insects (Tanglefoot Company, Grand Rapids, Michigan, USA). I reapplied Tanglefoot as needed and regularly cleared vegetation from around all plants and cylinders to prevent shading and inadvertent access by ants. To provide ants with access to plants, I placed short cylinders without Tanglefoot around plants and allowed the cylinder to rest on top of the soil surface. I also cleared vegetation from around ant access and control plants so that all plants were treated in the same way.

The cylinders effectively reduced visitation by ants and had no overall effect on predator richness. A combination of the Tanglefoot and clearing of vegetation from around cylinders greatly reduced the number of ants on ant exclusion plants. During the final census, ants were threefold more abundant on ant access plants (1.96 ± 0.15 ants/plant [mean ± SE]) than on ant exclusion plants (0.66 ± 0.12 ants/plant) (negative binomial model, $\chi^2 = 74.0$, $P < 0.001$, $N = 864$ plants). Periodically, surrounding vegetation fell onto experimental plants, providing ants with access to plants, but I regularly cleared vegetation and ants from plants to mitigate this potential problem. The presence or absence of predators on plants (logistic model, $\chi^2_1 = 0.71$, $P = 0.39$, $N = 864$ plants) and the number of predator species per plant (negative binomial model, $\chi^2_1 = 0.64$, $P = 0.42$, $N = 864$ plants) did not differ according to the ant treatment.

Measuring aphid population growth rate, ants, and predators.—I surveyed aphid populations, ants, and predators on all plants that were initially stocked with aphids (864 plants). The experimental design included 28 plant genotypes × 4 aphid densities × presence/absence of ants, for a total of 224 treatment combinations with 2–6 replicate plants (3.86 ± 0.03 plants) per treatment.

Two weeks following the addition of aphids, I counted all aphids on every plant by looking on both the upper and lower surfaces of every leaf. After five weeks, I counted the number of aphids again and terminated the experiment because I detected the first dispersal of aphids to control plants. This length of time (five weeks) allowed herbivore populations to grow for approximately three to five generations, based on a minimum generation time of seven days. During the final survey, I also recorded the number of ants and the number of predator species on every plant. The number of predator species is a good predictor of the number of predator individuals on *O. biennis* (Pearson correlation, $r = 0.93$, $P < 0.001$; Johnson et al. 2006), as there is typically just one individual per predator species on a plant. Finally, because multiple people counted aphids, I blocked by the person who counted aphids on a plant (counter).

I calculated per capita population growth rate of aphids on each plant and regressed this value against initial aphid density to test for density-dependent growth of aphid populations (Harrison and Cappuccino 1995, Agrawal et al. 2004). I calculated the daily per capita growth rate of aphids (dN/Ndt) as $(\ln[N_2] - \ln[N_1])/(t_2 - t_1)$, where N_2 and N_1 are the final and initial aphid densities on days t_2 and t_1, respectively. A negative relationship between daily per capita growth and initial density indicates that aphid population growth is negatively density dependent, a necessary condition for the density-dependent regulation of populations (Harrison and Cappuccino 1995). A statistical interaction between initial density and plant genotype would indicate that the strength of density dependence in population growth varied among plant genotypes.

To assess whether the factors affecting aphid populations varied as populations grew over time, I also partitioned population growth into two periods: the first two weeks (growth period 1, days 1–14) and the latter three weeks (growth period 2, days 15–35) of population growth. For growth period 2, the density of aphids on day 14 served as the initial density of aphids. This method of partitioning the growth of aphid populations into two growth periods also enabled me to better understand how a greater range of initial aphid densities affected the growth rate of populations, as the density of aphid populations at the beginning of growth period 2 spanned a greater range (1–200 aphids) than those manipulated at the beginning of growth period 1 (2–11 aphids).

Statistical analyses

I assessed the effects of plant genotype, initial aphid density, and ants on final aphid density and per capita aphid growth rate using restricted maximum likelihood (REML) in Proc Mixed of SAS (SAS Institute, Cary, North Carolina, USA). The full statistical model for analyses included all main effects, two-way and three-way interactions; higher order interactions were never significant. Initial density was entered into the model as a covariate, ant treatment and counter were fixed effects,

and all other factors and interactions were random effects. I sequentially deleted nonsignificant interactions ($P > 0.10$) between factors of primary interest (i.e., initial density, ants, and genotype) and the blocking factors (spatial block and counter). I then calculated the amount of variation explained by each significant effect as R^2 values derived from the sums of squares produced in the mixed-model component of Proc GLM of SAS.

To determine whether plant genotype affected ant abundance or predator species richness, I used generalized linear models in Proc Genmod of SAS (Allison 1999). The full model for analyses was: ant abundance or predator richness = ln(final aphid density + 1) + genotype + counter + block. Higher order interactions could not be included because of limitations with generalized linear models. Quadratic functions of aphid density were not significant and therefore were excluded from the final model. To assess the distribution that best fit the data, I examined the residuals for homogeneity of variance and the deviance statistic, which indicated that a negative binomial distribution and a Poisson distribution provided the best fit for ant abundance and predator richness, respectively (Allison 1999). I sequentially removed nonsignificant effects from the model. No ants occurred on one genotype (despite the presence of aphids), which made analyses intractable. To alleviate this problem, a single ant was added to a randomly chosen replicate of this genotype, which made tests for the effect of genotype slightly conservative.

Genetic variation in plant traits can directly and indirectly affect arthropods at the third trophic level (mutualistic ants and predators). For example, the number and type of trichomes on plants may directly affect the ability of predators to find and consume prey. Also, variation among plant genotypes that affects the growth and density of aphids can indirectly influence the third trophic level if ants and predators are attracted to higher densities of aphids. I distinguished between these direct and indirect effects by examining how the statistical significance (from Proc Genmod) and the amount of variance explained by plant genotype (calculated using REML) depended upon the inclusion of final aphid density as a covariate. I concluded that plant genotype had direct effects on ants and/or predators when genotype was statistically significant after accounting for final aphid density. I detected an indirect effect of plant genotype when the amount of variance explained by plant genotype significantly increased following the removal of aphid density from the model, which I assessed using the F_{max} test (Sokal and Rohlf 1995). This method does not account for indirect effects mediated by aphid performance (e.g., size, behavior, nutritional quality, etc.) that could be independent of aphid density.

Plant traits

Immediately preceding the final census of aphids, I measured seven traits from plants with 0 aphid density (control plants; 5–9 replicates per genotype): percentage of leaf water content, specific leaf area, total foliar carbon and nitrogen (as percentages of dry biomass), peroxidase activity (POD, a putative resistance protein), density of simple trichomes, and aboveground dry biomass. I also assayed foliar polyphenol oxidase, but found no activity. Because control plants received no aphids and little herbivory, these measurements should closely reflect constitutive levels of resistance traits. Percentage of leaf water content, specific leaf area, and trichome density were measured from leaf discs (26 mm^2) removed from fully expanded leaves. The wet and dry masses of leaf discs were measured to the nearest 10^{-5} g, and specific leaf area was calculated as: 0.26 cm^2/g dry mass. I counted trichomes from the lower surfaces of leaves because this is where aphids most commonly fed. To measure total carbon, total nitrogen, and peroxidase concentration, I collected expanding leaves and stored them at −80°C until analyses were performed. Percentages of total carbon and nitrogen were measured by microcombustion using 10 mg of dried ground leaf material in an Elemental Combustion System 4010 CHNS-0 analyzer (Costech Analytical Technologies, Valencia, California, USA). To assay peroxidase activity, I followed the methods of Thaler et al. (1996). Briefly, 0.1 g of leaf tissue was homogenized in ice-cold buffer and then centrifuged to obtain a clarified extract. I then added 10 μL of supernatant to a 2.92-mmol/L guiacol solution in pH 8 K Phos buffer with H_2O_2 added as a cofactor. The POD activity was measured as the increase in optical density at 470 nm using a PowerWaveX Microplate Scanning Spectrophotometer (Bio-Tek Instruments, Winousk, Vermont, USA).

I determined whether plant traits were genetically variable using REML in Proc Mixed of SAS (SAS Institute). Variables were transformed with square-root or ln transformations when needed to improve normality and homogeneity of variance. Restricted maximum likelihood was also used to calculate the genotypic best linear unbiased predictors (BLUPs; similar to the arithmetic mean) for each plant trait. With these BLUPs, I performed stepwise multiple regression to identify plant traits that genetically covaried with aphid per capita population growth rate, ant abundance, and predator richness. I used a criterion of $P < 0.15$ for entry into the multiple regression model. I removed one outlying genotype from analyses because aphid growth rate deviated from the predicted response by three standard deviations, which substantially reduced the fit of the model. The results with this genotype included in analyses are also reported.

Results

Aphid density

Aphid populations increased 31-fold during the experiment, and plant genotype had stronger effects on final aphid density than either initial density or

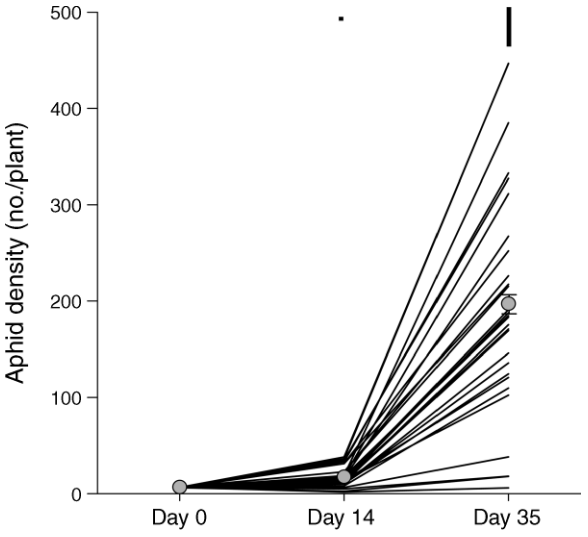

FIG. 1. Variation in aphid (*Aphis oestlundi*) density among plant genotypes (*Oenothera biennis*), studied at University of Toronto's Koffler Scientific Reserve at Jokers Hill in Ontario, Canada. Aphids were added to plants on day 0 and counted after two and five weeks of population growth. Each line represents the mean value for one of 28 plant genotypes calculated from the raw data. The circles are the numbers of aphids (mean ± SE; SE not visible at some time points) among all plants. The mean standard error of family means is displayed for day 14 (small point) and day 35 (bar) at the top of the figure.

mutualistic ants (Fig. 1; Appendix C). Plant genotype of *O. biennis* explained 27% of the total variation in final aphid density (Appendix C), with mean aphid density per plant ranging 75-fold among plant genotypes (Fig. 1). As expected, final aphid density increased with initial aphid density, but this effect explained just 6% of the total variation (Appendix C). The effects of ants on aphid density depended upon the initial density of aphids (initial aphid density × ant interaction; Appendix C). Overall, final aphid density was 19% lower in the presence of ants than in the absence of ants, but this effect explained <1% of the total variation in aphid density.

Aphid per capita population growth rate

Plant genotype affected aphid per capita population growth rate (genotypic range: 0–0.11 aphids·mother^{-1}·d^{-1}, SE = 0.01) independently of all other factors and explained 29% of the total variation in growth rate (Table 1). The strength of density dependence increased from the first growth period (slope = −0.001, SE = 0.001, $F_{1,41} = 0.53$, $P = 0.47$, $R^2 = 0.001$), when initial aphid density was low (2–11 aphids per plant), to the second growth period (slope = −0.003, SE = 0.002, $F_{1,27} = 32.16$, $P < 0.001$, $R^2 = 0.04$) when initial aphid density ranged more widely (1–200 aphids). The effect of initial density was weakly significant over the entire length of the experiment (Table 1).

The presence or absence of ants determined whether aphid populations experienced density-dependent or density-independent growth (i.e., initial aphid density × ant interaction; Table 1). In the absence of ants, aphid populations grew in a negatively density-dependent manner (slope = −0.002, SE = 0.001, $F_{1,399} = 8.48$, $P = 0.004$, $R^2 = 0.02$; Fig. 2). In the presence of ants, aphid population growth was density independent (slope = 0.0004, SE = 0.001, $F_{1,45} = 0.41$, $P = 0.53$, $R^2 = 0.001$). Although the interaction between initial aphid density and ants was statistically significant (Table 1), it accounted for a small fraction of the total variation in aphid growth rate ($R^2 = 0.005$).

The mutualistic benefit of ants to aphids depended upon initial aphid density (Table 1, Fig. 2). At low initial aphid densities, aphid populations grew significantly faster in the absence of ants (i.e., where 95% CI do not overlap in Fig. 2), suggesting a net cost of ant tending.

TABLE 1. The effects of initial aphid (*Aphis oestlundi*) density, ants, and plant genotype (*Oenothera biennis*) on the per capita population growth rate of aphids.

Factor	VC	F/χ^2	P	Variance (%)
Initial density (density)†		2.87	0.09	0.2
Ants†		10.16	**0.002**	0.9
Genotype†	6.98×10^{-4}	32.4	**<0.001**	28.9
Counter†		4.62	**0.01**	0.8
Block	0.72×10^{-4}	20.4	**<0.001**	2.3
Density × ants†		6.29	**0.01**	0.5
Density × genotype	0	0		
Ants × genotype	0.2×10^{-4}	0.4	0.26	
Residual	16.29×10^{-4}			

Notes: Results are for aphid population growth over the entire duration of the experiment. Spatial block (block) and the person who counted aphids on a plant (counter) were included as blocking factors. I calculated the percentage of variation explained by all main effects and significant interactions using general linear models using the equation: (treatment sums of squares)/(total sums of squares) × 100%. Variance components (VC) for random effects are also provided. Significant effects ($P < 0.05$) appear in boldface type. This research was conducted at University of Toronto's Koffler Scientific Reserve at Jokers Hill in Ontario, Canada.

† A fixed effect in which I assessed the statistical significance using an F statistic. All other effects in the model were random, and significance was tested using a χ^2 statistic from log-likelihood ratio tests.

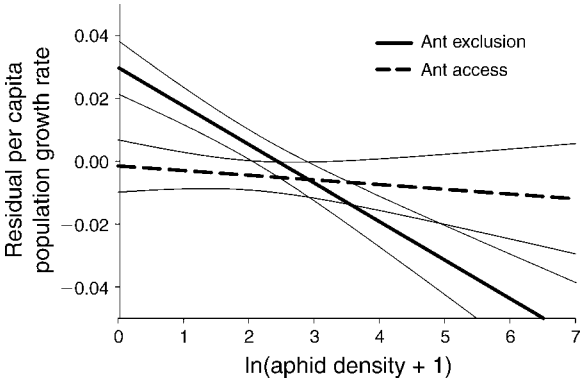

FIG. 2. The effect of ants on growth of aphid populations. Per capita aphid population growth rate is plotted against ln(initial aphid density + 1) for growth period 2, where initial aphid density is the density of aphids at the end of growth period 1. Each heavy line represents the regression line (with ±95% CI shown by lighter lines) through the residual growth rate, with the variance due to plant genotype, counter, and block partitioned out. A negative regression slope indicates negative density dependence. There are significant ($P < 0.05$) differences in growth rate when the 95% CIs do not overlap at a given density; differences are increasingly significant with greater disparity between the 95% CIs. Individual data points are omitted for illustrative purposes.

At high aphid densities, aphid populations grew faster in the presence of ants, consistent with a mutualistic benefit of ant tending (Fig. 2). Although the main effect of ants and the density × ant interaction were significant, they only accounted for 0.9% and 0.5% of the total variation in aphid growth rate, respectively.

Genetically variable plant traits and aphid population growth rate

Oenothera biennis exhibited significant broad-sense heritability for six of the seven traits measured (Appendix B). Genetic variation in percentage of leaf water content, trichome density, and percentage of leaf nitrogen accounted for 49% of the variation in per capita aphid population growth rate (multiple regression model, $F_{3,26} = 7.45$, $P = 0.001$, $R^2 = 0.49$). Percentage of leaf water content (slope = 0.67, $t = 2.82$, $P = 0.01$, partial $R^2 = 0.22$) and trichome density (slope = 0.005, $t = 2.57$, $P = 0.02$, partial $R^2 = 0.14$) positively covaried with aphid growth rate, while percentage of leaf nitrogen negatively covaried with aphid growth rate (slope = −0.21, $t = -2.45$, $P = 0.02$, partial $R^2 = 0.13$; Fig. 3). Only percentage of leaf water content significantly predicted population growth rate when I included the outlying genotype in the model.

Plant genetic effects on ants

Plant genotype of *O. biennis* and final aphid density both predicted variation in the abundance of ants on plants (Table 2). The mean number of ants per plant varied from 0 to 3.4 among plant genotypes, and ant abundance responded positively to increased aphid density (Appendix D). Plant genotype explained signif-

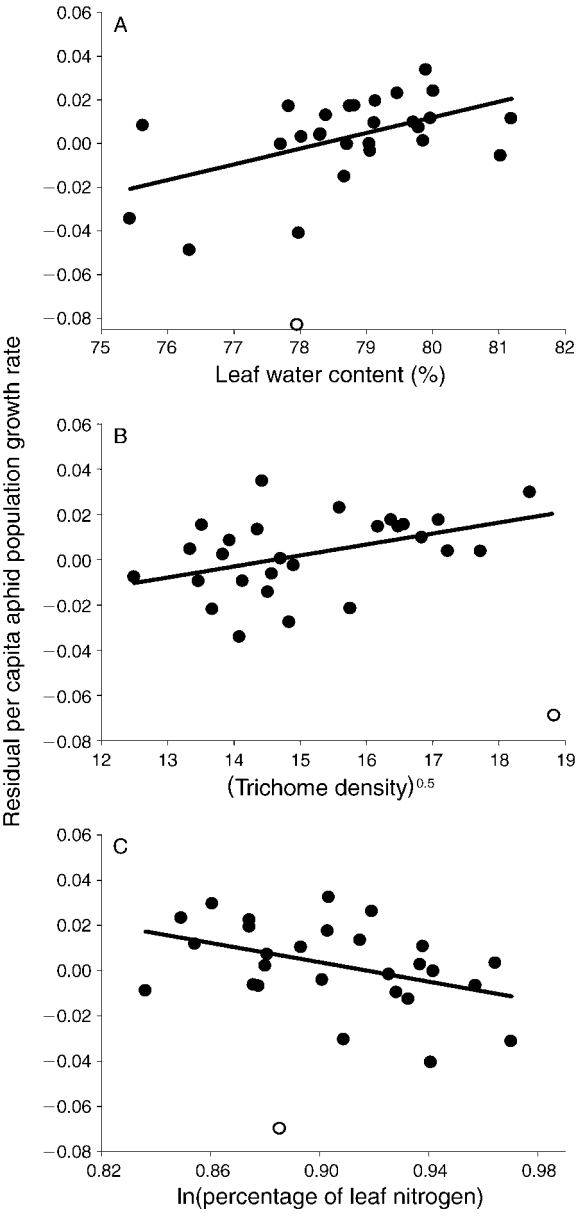

FIG. 3. Regression of per capita aphid population growth rate against genetic variation in plant traits. Multiple regression showed that the percentage of leaf water content and trichome density were positively associated with growth rate, whereas the percentage of nitrogen was negatively related to growth rate. Figures depict the partial correlations, which are plotted as residual growth rate (i.e., variation due to other significant independent variables was removed) vs. the trait. Each point is the best linear unbiased predictor (BLUP) for a genotype. The open circle in each panel represents a single outlying genotype excluded from the analysis. To reduce heteroscedasticity and improve normality, trichome density (no./26 mm^2) was square-root transformed.

icant variation in ant abundance (plant genotype, $\sigma^2 = 0.012$, SE = 0.01) when I included aphid density in the analysis (Table 2). When I removed aphid density from the model, plant genotype explained significantly more

variation in ant abundance (plant genotype, $\sigma^2 = 0.094$, SE = 0.035; F_{max} test = 7.86, $P < 0.01$), and its statistical significance became even stronger ($\chi^2_{27} = 121.75$, $P < 0.001$). These results show that plant genotype had direct effects on ant abundance, as well as indirect effects mediated through aphid density.

Multiple regression revealed that genetic variation in trichome density was positively related to the number of ants on plants (slope = 0.09, $t = 2.61$, $P = 0.02$, partial $R^2 = 0.30$), while percentage of carbon content (slope = −0.51, $t = -2.60$, $P = 0.02$, partial $R^2 = 0.19$) and peroxidase activity (slope = −0.66, $t = -2.16$, $P = 0.04$, partial $R^2 = 0.09$) negatively covaried with ant abundance. When I included final aphid density in the model the relationship with trichome density remained significantly positive (slope = 0.05, $t = 2.46$, $P = 0.02$, partial $R^2 = 0.04$), but the other traits became nonsignificant ($P > 0.10$).

Plant genetic effects on predators

Plant genotype and final aphid density affected predator species richness in the absence of ants, but these factors had no detectable effect on predators in the presence of ants (Table 2). The number of predator species varied sixfold among plant genotypes (plant genotype, $\sigma^2 = 9.98 \times 10^{-3}$, SE = 0.005) when ants were excluded from plants, and predator richness increased with aphid density (Appendix D). When I removed aphid density from the model, the statistical significance of plant genotype ($\chi^2_{27} = 46.13$, $P = 0.01$) and the amount of variation explained in predator richness (plant genotype, $\sigma^2 = 11.71 \times 10^{-3}$, SE = 0.006) increased, but this increase in variance attributed to plant genotype was not significant (F_{max} test = 1.17, $P > 0.05$). Therefore, plant genotype and aphid density had independent direct effects on the number of predator species in the absence of ants. None of the plant traits measured was a significant predictor of variation in predator richness (results not shown).

Discussion

Plant genotype of *Oenothera biennis* strongly affected the growth of aphid populations, the abundance of aphid-tending ants, and the number of predator species. Three results are noteworthy. First, plant genotype affected aphid per capita population growth rate independently of all other factors and explained more variation than aphid density and mutualistic interactions (Table 1). Second, genetic variation in three plant traits (percentage of leaf water content, trichome density, and percentage of leaf nitrogen) accounted for nearly half of the variation in aphid growth rate among plant genotypes (Fig. 3). Third, plant genotype had direct effects on ant abundance and predator species richness, as well as an indirect effect on ants, which was mediated by variation in aphid density (Table 2). Together these results show that genetic variation in plant quality can be one of the most important factors governing herbivore population dynamics and tritrophic interactions.

Table 2. The effects of final aphid density and plant genotype on ant abundance and the number of predator species.

Factor	df	χ^2	*P*
Ant abundance			
Final aphid density	1	183.27	**<0.001**
Genotype	27	42.63	**0.03**
Block	3	8.08	**0.04**
Predator species			
Ant access			
Final aphid density	1	0.92	0.34
Genotype	27	21.85	0.74
Counter	2	13.07	**0.002**
Ant exclusion			
Final aphid density	1	12.09	**0.001**
Genotype	27	42.83	**0.03**
Counter	2	10.93	**0.03**

Note: Spatial block (block) and the person who counted the aphids and predators (counter) were included as blocking factors if $P < 0.05$; otherwise they were removed from the model. Analyses were performed using generalized linear models (see *Materials and methods*).

Importance of plant genotype for herbivore populations

Ecologists have long debated the importance of density-dependent (Nicholson 1933, Southwood and Comins 1976) vs. density-independent (Andrewartha and Birch 1954) factors in affecting the size and dynamics of herbivore populations. In this study, plant genotype was a density-independent factor because genotype and initial aphid density did not interact. Surprisingly, I found that plant genotype was more important than density-dependent factors in affecting the per capita growth rate of a specialist insect herbivore over the range of densities used in this experiment. This result adds to growing evidence that intraspecific genetic variation in plant traits can be a key determinant of the distribution, abundance, and dynamics of arthropod populations on plants (Karban 1992, Fritz and Hochwender 2005, Whitham et al. 2006, Johnson and Stinchcombe 2007).

My results also show that plant genotype has a stronger effect on herbivore population growth than the effects of mutualistic ants. Only one previous study examined the combined effects of plant genotype and mutualistic interactions on herbivore population dynamics in a natural system (Wimp and Whitham 2001). Variation among hybrid and parental genotypes of poplar trees and aphid-tending ants had large effects on the fecundity and distribution of a specialist aphid. As with my study, poplar genotype and mutualistic ants did not interact to affect aphids. The consistency in these results suggests that genetic variation in plant traits may frequently affect the growth of aphid populations in ways that are independent of density-dependent factors and ant–aphid mutualisms (but see Underwood and Rausher 2000).

Intraspecific and interspecific genetic variation in plant traits

This study shows how intraspecific genetic variation in specific plant traits predicts aphid population growth, and it highlights how variation in plant traits within and between plant species can have similar effects on herbivores. For example, I found that increased trichome density positively covaried with aphid population growth rate. A similar relationship was found across 18 species of milkweeds (Agrawal 2004). Although neither study identified the specific mechanism underlying this relationship, increased trichome density can reduce predation rates (Price et al. 1980, Bottrell et al. 1998). In the *Aphis–Oenothera* system, early instar nymphs are small and frequently feed beneath a cover of glandular and/or non-glandular trichomes, where higher trichome densities may provide aphids with protection from predators. I also detected a positive relationship between population growth rate and leaf water content. In a similar way, increased leaf water content among different plant species positively affected growth and nitrogen assimilation by Lepidoptera larvae (Scriber and Feeny 1979), suggesting that greater water content in leaves may allow aphids to process nitrogen and sugars more efficiently. Surprisingly, my results do not support the prediction that increased nitrogen positively affects aphid growth rate (Mattson 1980, White 1984, Agrawal 2004). In fact, I found the opposite pattern. This discrepancy may simply be due to my measurement of total nitrogen in leaves, which may not correlate with the concentration of soluble nitrogen available to aphids in phloem.

Genetic variation in plant traits predicted variation in the abundance of ants, even after taking final aphid density into account. Some plants have evolved the ability to attract ants with specialized food rewards, like extra-floral nectar (Rudgers 2004), or protective structures that house ant colonies (Janzen 1966). The morphological and chemical traits that covaried with the number of ants on *O. biennis* are not specialized for attracting ants. The covariation between these traits and ant abundance illustrates the manner in which genetic variation in many plant traits, not just specialized structures, can influence the mutualists of herbivores.

Top-down effects of ants and generalist predators on aphids

Ant–aphid associations are thought to be mutualistic, with ants and aphids having reciprocal positive fitness effects on one another (Stadler and Dixon 2005). There is mounting evidence, however, that tending ants can negatively affect aphid fitness (Stadler and Dixon 1998, Yao et al. 2000, Katayama and Suzuki 2002). These costs of ant tending are thought to be conditional on the density of aphids, the density and effectiveness of ants as mutualists, and the presence of predators (Stadler and Dixon 2005). For example, Yao et al. (2000) found that aphid tending reduced the size of individual aphids and the number of embryos produced by each aphid, but this cost was offset by the protection ants provided aphids against predators.

I detected complex effects of ants on aphid populations, which involved both net costs and benefits depending upon initial aphid density (Fig. 2). Ants reduced the strength of negative density-dependent growth of aphid populations, possibly by reducing density-dependent mortality by predators. This result is opposite to a similar ant–aphid system (Breton and Addicott 1992*a*) in which ant tending increased the strength of negative density dependence. The lack of a density-dependent response by predators in the system studied by Breton and Addicott (1992*a*) may explain this difference.

The presence of ants caused density-independent growth of aphid populations, which was associated with a statistically significant net cost of ant tending at low aphid densities (1–6 aphids per plant) and a significant benefit of ant tending at high aphid density (>145 aphids per plant; Fig. 2). These results are consistent with the findings from a similar ant-tended aphid (Katayama and Suzuki 2002). Katayama and Suzuki (2002) showed that tended ants excrete more honeydew and suffered proportionately higher predation at low densities than at high densities (Katayama and Suzuki 2002). The increased secretion is expected to impose a physiological cost on reproduction (Katayama and Suzuki 2002, Stadler et al. 2002), and disproportionate predation at low aphid densities is most likely when the response of ants to aphids is density dependent (Appendix D). My results are consistent with density-dependent recruitment of ants providing aphids with greater protection from predators at high aphid densities than at low densities, tipping the effects of tending from a net cost to a net benefit. Although the effects of ants on aphids reported in this study are biologically interesting, I do not believe they are biologically important in the *Aphis–Oenothera* system when compared to the effects of plant genotype, as ants had a very small effect on aphid growth rate and variation in the strength of density dependence (Table 2).

Effects of plant genotype on tritrophic interactions

Genetic variation in a plant population can have direct and indirect ecological effects across multiple trophic levels when phenotypic differences among plant genotypes affects the abundance or diversity of the mutualists and natural enemies of herbivores. Such phenomena are well known in agricultural systems, in which agronomists have tried to use a combination of plant resistance and biocontrol agents to reduce herbivory (Bottrell et al. 1998, Hare 2002). In contrast, our understanding of the community genetics of tritrophic interactions in natural systems is incomplete, as most studies have been conducted on gall-forming herbivores and their parasitoids or predators (Weis and Abrahamson 1986, Fritz 1995, Stiling and Rossi 1996, Fritz et al. 1997, Bailey et al. 2006; but see Wimp and

Whitham 2001). My results show that plant genotype can directly influence the abundance of aphid-tending ants and generalist predators, as well as indirectly affect ant mutualists through effects on aphid density.

Conclusions

I show that plant genotype has strong bottom-up effects across multiple trophic levels, which are independent of density-dependent factors and mutualistic interactions with aphid-tending ants. Although negative density-dependent growth and ants affected aphid populations, the density-independent effects of plant genotype had primacy in affecting the growth of aphid populations over multiple generations. These results indicate that the bottom-up effects of genetic variation in plant traits can be one of the most important factors affecting the population growth of a specialist herbivore, as well as the abundance and species richness of mutualists and predators, respectively. As such, studying the community-level consequences of genetic variation in plant traits may be essential to understanding the ecology of plant–arthropod interactions.

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APPENDIX A

A photograph of aphids (*Aphis oestlundi*) and ants (*Crematogaster lineolata*) interacting on evening primrose (*Ecological Archives* E089-007-A1).

APPENDIX B

Descriptive statistics for the effects of plant genotype on plant traits (*Ecological Archives* E089-007-A2).

APPENDIX C

The effects of aphid density, ants, and plant genotype on the final number of aphids per plant (*Ecological Archives* E089-007-A3).

APPENDIX D

The response of ant abundance and predator diversity to final aphid density (*Ecological Archives* E089-007-A4).

***Ecological Archives* E089-007-A1**

Marc T. J. Johnson. 2008. Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology* 89:145–154.

Appendix A. A photo of the aphid *Aphis oestlundi* and the ant *Crematogaster lineolata* interacting on evening primrose.

Aphis oestlundi being tended by the ant *Crematogaster lineolata* on an evening primrose plant in the field. Aphids taken from this plant were used to start the aphid colony. Photo credit: Emily Darling.

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Ecological Archives E089-007-A2

Marc T. J. Johnson. 2008. Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology* 89:145–154.

Appendix B. Descriptive statistics for the effects of plant genotype on plant traits.

TABLE B1. Descriptive statistics for the effects of plant genotype on plant traits.Included are the range of breed values for each trait, variance explained by plant genotype (VC), the coefficient of genetic variation (CV_g), broad-sense heritability (H^2), and the χ^2 and *P* value from a log-likelihood ratio test for the effect of plant genotype. I measured traits from plants that received zero aphids. Significant effects ($P < 0.05$) are in bold.

Plant trait	Range	VC	CV_g	H^2	χ^2	*P*
Leaf water content (%)	75.4 – 81.2	3.15	2.18	0.1	9.4	**0.001**
Specific leaf area	240.1 – 283.4	265.39	4.41	0.08	4.5	**0.02**
Leaf carbon (%)	43.9 – 44.5	0.11	0.76	0.21	1.4	0.12
Leaf nitrogen (%)	2.4 – 2.6	0.02	4.96	0.14	3.8	**0.03**
Peroxidase	2.0 – 3.4	0.23	22.65	0.07	6.4	**0.006**
Trichome density	163.5 – 364.9	3148.88	23.65	0.54	30.9	**<0.001**
Plant dry biomass	5.3 – 10.0	2.17	18.03	0.2	6.2	**0.006**

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Ecological Archives E089-007-A3

Marc T. J. Johnson. 2008. Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology* 89:145–154.

Appendix C. The effects of aphid density, ants, and plant genotype on the final number of aphids per plant.

TABLE C1. The effects of initial aphid density, the presence/absence of ants, and plant genotype on the final number of aphids per plant. Spatial block and the person who counted aphids on a plant (counter) were included as blocking factors. I calculated the percent variation (% Var) explained by all main effects and significant interactions using general linear models using the equation: (factor-sums of squares)/(total sums of squares) × 100%. The variance components (VC) for all random effects are also provided. Significant effects ($P < 0.05$) are in bold.

Source	VC	F/ χ^2	P	% Var
Initial density (density)†		76.52	**<0.001**	6
Ants†		9.14	**0.003**	0.8
Genotype	0.84	31.3	**<0.001**	27.1
Block	0.1	22.1	**<0.001**	2.3
Counter†		1.12	0.33	0.6
Density × Ants†		5.47	**0.02**	0.5
Density × genotype	<0.01	0	-	-
Ants × genotype	0.03	0.5	0.24	-
Ants × counter†		3.55	**0.03**	0.2
Density × ants × counter†		2.18	0.07	-
Residual	1.99			

† Denotes fixed effect in which the significance was assessed using an F statistic. All other effects in the model were random and their significance was tested using a χ^2-statistic from log-likelihood ratio tests.

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Ecological Archives **E089-007-A4**

Marc T. J. Johnson. 2008. Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology* 89:145–154.

Appendix D. The response of ant abundance and predator diversity to final aphid density.

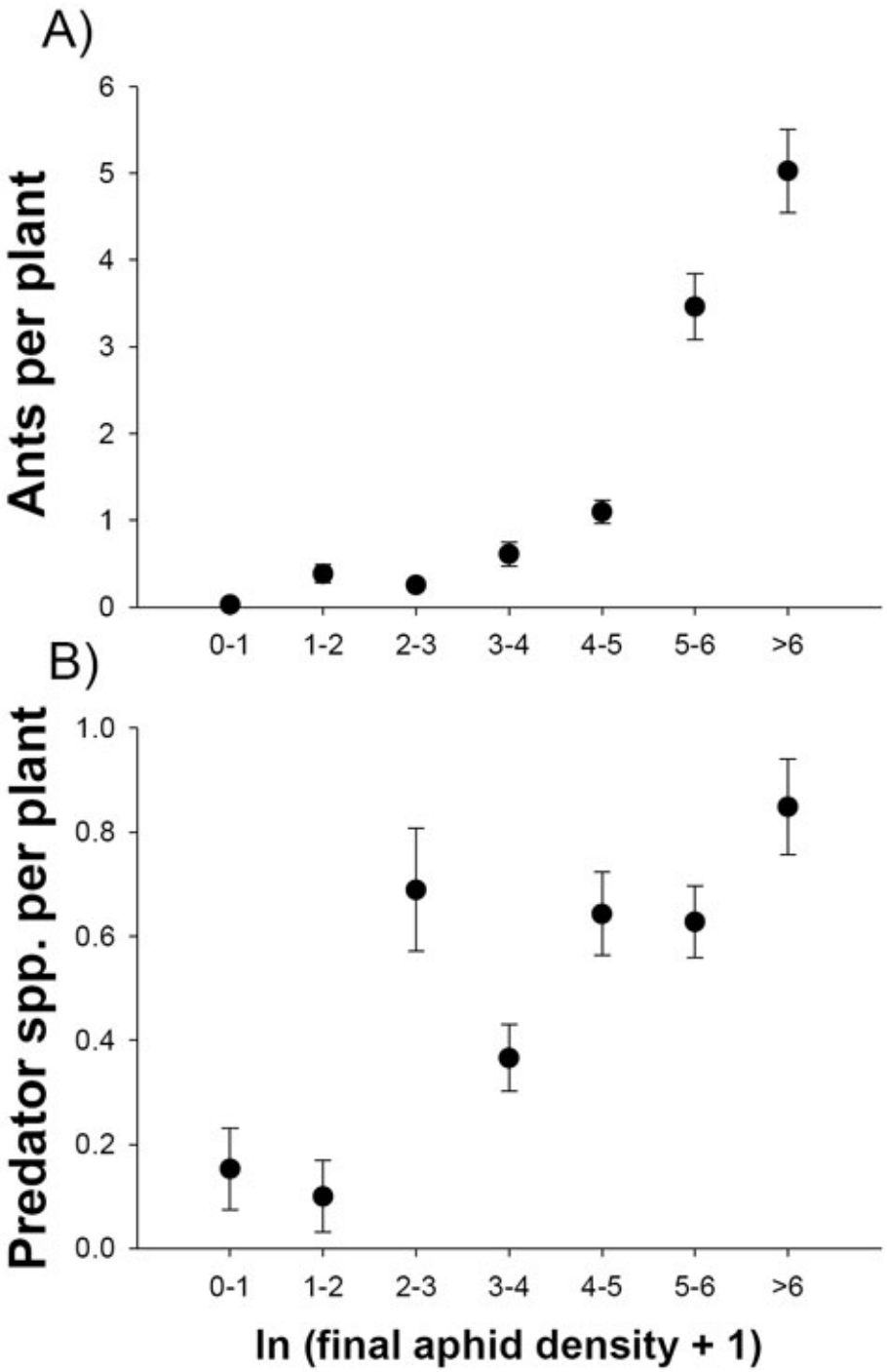

FIG. D1. The response of ant abundance and predator diversity to final aphid density. The (A) mean number of ants per plant (ant access plants) and (B) the number of predator species per plant (ant exclusion plants) are plotted against ln(final aphid density +1) per plant. Values on the *x* axis are binned for illustrative purposes.

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