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Effect of genetic variance in plant quality on the population dynamics of a herbivorous insect

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Summary

1. Species diversity can affect many ecological processes; much less is known about the importance of population genetic diversity, particularly for the population dynamics of associated species. Genetic diversity within a host species can create habitat diversity; when associated species move among hosts, this variation could affect populations additively (an effect of average habitat) or non-additively (an effect of habitat variance). Mathematical theory suggests that non-additive effects of variance among patches should influence population size, but this theory has not been tested.

2. This prediction was tested in the field by asking whether aphid population dynamics parameters on strawberry plant genotype mixtures were additive or non-additive functions of parameters on individual plant genotypes in monoculture using model fitting.

3. Results show that variance in quality among plant genotypes can have non-additive effects on aphid populations, and that the form of this effect depends on the particular plant genotypes involved.

4. Genetic variation among plants also influenced the spatial distribution of aphids within plant populations, but the number of plant genotypes per population did not affect aphid populations.

5. These results suggest that predicting the behaviour of populations in heterogeneous environments can require knowledge of both average habitat quality and variance in quality.

Key-words: *Chaetosiphon fragaefolii*, *Fragaria chiloensis*, genetic diversity, non-additive effects, plant-insect interactions

Introduction

Ecologists addressing a range of different questions are interested in how biodiversity (population or community level variance) may affect ecological processes, from the influence of species diversity on productivity to the influence of genetic diversity on resilience after disturbance. One rarely studied effect of species or genetic diversity is on the population dynamics of associated species. A diverse population of hosts creates variation in habitat quality for associated species, just as abiotic conditions might create variation in habitat quality among patches within metapopulations or metacommunities (see, e.g. the idea that local populations can be sources or sinks; Pulliam 1988). When organisms move among patches, so that individuals experience this variation, variation can have additive and/or non-additive effects on the dynamics of the population (Hughes *et al.* 2008). Under additive effects, the equilibrium size of a population across a mixture of patch types equals the sum of population sizes on the individual patch types in isolation; that is, population size can be predicted by only average habitat quality. With non-additive effects, the population equilibrium across a mixture of patches would deviate from the additive expectation (Helms & Hunter 2005); that is, the population would be affected by both average habitat quality and variance in quality. Models (e.g. Holt 1985; Pulliam 1988; Hastings 1993; Ruel & Ayres 1999; Underwood 2004) show that variance in habitat quality (whether biotic or abiotic) within a population can influence population dynamics, but empirical tests of this idea are logistically difficult in most systems. In general, work on the ecological consequences of biodiversity has focused less on population dynamics, and more on aggregate responses such as productivity or the species richness of associated species, often without distinguishing additive from non-additive mechanisms of diversity effects (Hughes *et al.* 2008).

Herbivorous insects and their host plants are excellent systems for examining the effect of variation in habitat quality on population dynamics. Individual plant species and genotypes differ in traits that influence their quality as herbivore

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habitat (e.g. Zangerl & Berenbaum 1991; Fritz & Simms 1992), and these differences can affect long-term herbivore population dynamics (e.g. Hunter & Price 1992; Ylioja *et al.* 1999; Underwood & Rausher 2000; Underwood 2007). A large literature compares insect incidence in agricultural monocultures (containing one plant genotype or species) with not in polycultures (containing more than one plant type) (Andow 1991). Although rarely directly addressing effects of variance in plant quality or fully characterizing population dynamics, these studies suggest a practical application (i.e. pest reduction) for understanding effects of variance in plant–insect herbivore systems.

Variance among plants might influence herbivore population size for many reasons. For plant populations of equal mean quality, herbivore populations might increase with variance in plant quality if herbivores feed selectively on high-quality plants. Alternatively, herbivore populations might decrease as variance increases if variation in plant quality increases the ratio of herbivore movement to feeding time (Bernays 1999) or decreases herbivore digestive performance (Stockhoff 1993). Non-additive effects in plant mixtures might also arise from two theoretical mechanisms: source-sink dynamics between high- and low-quality plants (Underwood 2004) and Jensen's inequality (Ruel & Ayres 1999; Inouye 2005). When herbivores move among plants, source-sink dynamics may lead to non-additive effects. If herbivore populations on individual plants have logistic population growth, then herbivore subpopulations on high-quality plants should have higher values of r and/or K than subpopulations on low-quality plants. Depending on the correlation between r and K across plants in a mixture, variance in plant quality can lead to larger or smaller equilibrium population sizes than expected from additive effects alone (Underwood 2004). Jensen's inequality suggests that average population size on a plant mixture will differ from the population predicted by average quality when plant quality and herbivore population size are related by a nonlinear function; the degree and direction of the deviation depends on the degree of nonlinearity and whether it is concave or convex.

Although non-additive effects of variation in plant quality are to be expected due to several different mechanisms, few empirical studies have directly addressed the effect of variance in plant quality on herbivore populations (but see Power 1988; Crawford, Crutsinger & Sanders 2007). Most studies of how herbivores are affected by plant mixtures have asked how herbivores are influenced by the *number* of plant types in a mixture, using polycultures of crop species (by far the most common type of study, see Andow 1991 for review), genotype mixtures within crop species (e.g. Altieri & Schmidt 1987; Gold, Altieri & Bellotti 1989), and mixtures of plant phenotypes (Kareiva 1982). These studies suggest that mixing different plant types can affect herbivore numbers, and effects can be negative or positive (Andow 1991). Most of these studies did not test for non-additive effects, however, so they cannot distinguish additive effects of the number of plant types in a mixture from effects of variance per se. Recent studies have addressed non-additive effects of plant mixtures on responses other than population dynamics such as richness of associated arthropods and plant productivity (Crutsinger *et al.* 2006; Johnson, Lajeunesse & Agrawal 2006).

I conducted a field experiment with wild strawberry (*Fragaria chiloensis* (L.) Duchesne) and strawberry aphids (*Chaetosiphon fragaefolii* Cockerell) to address four questions about the effects of plant population genetic variation on herbivore population dynamics:

1. Do the dynamics of aphid populations (summarized by the parameters of a population-dynamics model) on mixtures of strawberry genotypes differ from the average of dynamics on the monocultures contributing to those mixtures (i.e. is there a non-additive effect of variance)?

2. Are the effects of variance negative or positive (i.e. are aphid populations on plant mixtures larger or smaller than expected under additive effects)?

3. Does plant genetic diversity (measured as number of genotypes) affect aphid population size?

4. How is aphid distribution within plant populations related to the effect of variance in plant quality on aphid populations?

Materials and methods

EXPERIMENTAL SYSTEM

Wild strawberry and strawberry aphids are native and active year round in coastal California, where this research was carried out. Strawberry aphids are specialists on the genus *Fragaria* and do not alternate hosts. Despite the ability of *F. chiloensis* to reproduce asexually through runners, strawberry populations show substantial genetic variation (Alpert, Lumaret & Di Giusto 1993). Genotypes for this experiment were collected in the field (Sonoma County, California, USA, genotypes 'Wrights 2,' 'Doran 1,' and 'Doran 3') and obtained from the US Department of Agriculture National Clonal Germplasm Repository (Corvallis, OR, USA, genotypes '34,' '55,' '361,' '1312,' '59,' '46,' '340,' '39,' and '37'; genotype numbers refer to Germplasm Repository inventory ID numbers). All plants used in this experiment resulted from several rounds of asexual propagation in a common greenhouse environment at the University of California, Davis. During propagation, plants were rooted in 3·8 × 21-cm plastic tubes (Cone-tainers, Stuewe & Sons, Corvallis, OR, USA) in potting mix and watered and fertilized as needed with Miracle-Gro (Scotts Company, Marysville, OH, USA). Strawberry aphids were collected from multiple populations in the field (Sonoma County, CA) and reared for several generations in the greenhouse on a shifting mixture of wild and cultivated strawberry genotypes, none of which were used in this experiment. This procedure was designed to prevent the development of a feeding preference for the plant genotypes used in the experiment. Alates were absent in this experiment, but both adult and early instar aphids walk among nearby plants in the field, even when plants are not touching (N. Underwood, personal observation). The generation time of the aphids under the conditions of this experiment was about two weeks.

EXPERIMENT

I used an experimental design based on six strawberry genotypes known from greenhouse experiments to differ in quality as hosts for strawberry aphids, divided into two sets of three genotypes each

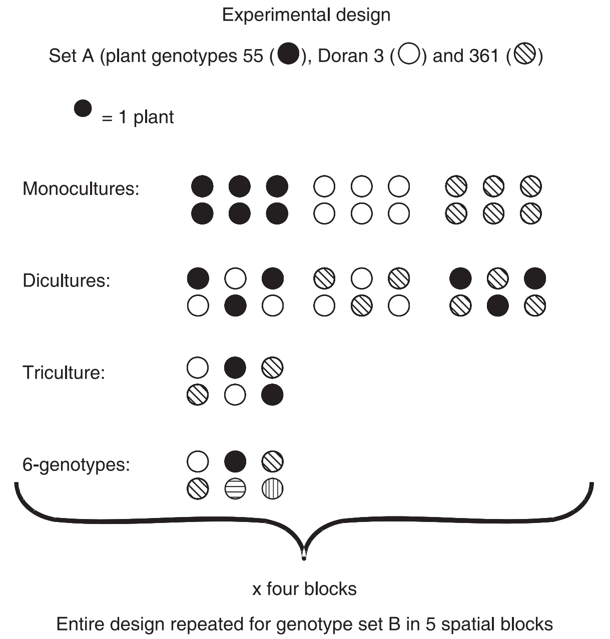

Fig. 1. Diagram of experimental design for one set of three plant genotypes. The full experiment included two sets of plant genotypes (A and B).

(Underwood 2007). Note that in this study, I define plant quality by aphid population response, rather than by measures of particular plant traits; the plant traits influencing quality in this experiment are unknown. Set A included genotypes 1312, 34, and Wright 2, and set B included genotypes 55, 361, and Doran 3. In the field, I created eight types of six-plant populations using each set of three genotypes separately: monocultures of each genotype, all possible dicultures within each set, a mixture of all three genotypes (triculture) for each set, and a six-genotype mixture for each set constructed by adding three additional genotypes (genotypes added for set A: 37, Doran 1, 59; genotypes added for set B: 39, 340, 46). The number of individuals was limited for particular genotypes, therefore six-genotype treatments included genotypes for which I was unable to construct monocultures. The full design was replicated across four randomized spatial blocks for set A and five blocks for set B, yielding 72 plant populations (Fig. 1). This design allowed me to address whether plant diversity had a non-additive effect on aphid populations (questions one and two) by using the monoculture populations to generate the expected population-dynamics model parameters for the di- and tricultures and testing the parameters estimated from the observed dynamics in those mixtures against their additive expectations. I could determine how the number of plant genotypes in a population influences aphid populations (question three) by comparing plant populations with one, two, three, and six genotypes. The experiment was conducted on March–September of 2000 in dune habitat at the University of California Bodega Marine Reserve (Sonoma County, CA, USA). Plants were transplanted to the field in Cone-tainers, which reduced root interaction and assisted with identification of individuals. Sand covered the Cone-tainer top, but not the plant crown. Plants rooted out the bottoms and tops of their cone-tainers. Plants were watered approximately weekly during the experiment. Cages of 2·5-cm wire mesh protected the plants from grazing mammals, but did not prevent access by invertebrates. The populations were planted in open areas between existing larger plants (primarily *Ammophila arenaria*, *Lupinus arboreus*, and *Baccharis pilularis*). If larger plants grew to overhang experimental populations, they were trimmed. Smaller plants (e.g. small grasses, *Camissonia cheiranthifolia*, *Gilia millefoliata*) grew within the populations.

Each experimental population consisted of six plants in two parallel rows of three (Fig. 1); neighbouring plants were separated by approximately 5 cm. As plants grew, their leaves often overlapped. After plants established, plant size was estimated as the sum of the sizes of all leaves, with leaf size measured as the length of the central leaflet midrib (this value is strongly correlated with leaf area, $r^2 = 0{\cdot}8$). Plant populations were spaced at least 1·5 m apart and blocks were at least 5 m apart. No natural strawberry-aphid populations occurred in the dunes where the experiment was conducted. The absence of aphids from all experimental plants was confirmed before the experiment began. Aphid migration from outside the experiment, or between populations within the experiment, was highly unlikely, but movement within populations was expected; preliminary experiments showed no colonization of plants 1 m or more from a plant with aphids over several months, but approximately 50% of aphids recovered in preliminary experiments had moved to new plants between 5 cm and 20 cm from their release plant over 3 days (N. Underwood, unpublished data). The movement rate in the experiment reported here was likely higher than in preliminary experiments as some plants within populations had leaves touching, however it was not logistically possible to estimate movement rates quantitatively during the experiment. I did directly observe aphids moving among plants within experimental populations (walking off one plant and arriving at another), and was able to infer movement indirectly by the locations of aphids from one census to the next.

I initiated aphid populations by placing one adult from the greenhouse colony on each plant and re-introduced aphids at the same density if populations went extinct. There were 16 aphid population extinctions during the experiment, occurring on eight of the 72 plant populations. Ten extinctions were on monocultures of '55', three were on monocultures of '1312' and three were on various mixtures. Each population was censused nine times (approximately every two weeks, April–July). At each census, every leaf of each plant was searched and every aphid counted. Other herbivores (other aphids, slugs, rabbits, and leafhoppers) and generalist predators (ground beetles, spiders, and pseudoscorpions) were noted, but too rare for formal analysis; no differences were noticed among plant population types. No parasitoids or parasitized aphids were observed during the experiment or subsequently at this site. Although strawberry aphids have five instars, I could reliably distinguish only three sizes: large (adult), medium, and small (probably first instar). Here, I consider total aphid numbers; future analyses will include size-structured data.

ANALYSES

To address question 1 ('do aphid dynamics on mixtures differ from those on monocultures?'), and to provide estimates of aphid carrying capacities for subsequent analyses, I estimated population-dynamic parameters for the aphid population on each type of strawberry population. I used maximum likelihood (Edwards 1992) to fit a series of population-dynamic models to the data for each population type (using monocultures, dicultures and tricultures). I first considered alternative model structures. A model fitting only the mean population size with associated error ('mean only model', $dN/dt = \bar{N}$) and an exponential growth model ($dN/dt = rN$) were alternatives with no density dependence, while the Ricker ($N_{t+1} = N_t re^{(-bN_t)}$) and logistic ($dN/dt = rN(1\text{–}N/K)$) models (Edelstein-Keshet 1988) were density-dependent alternatives, each using either Poisson or lognormal observation or process error. In these models, N represents aphid population size, r represents maximum per-capita population growth rates, b represents the strength of density dependence, K represents carrying capacity, and t indicates time-step. Models where the variance was a function of population size were also considered, but did not result in improved fits.

The logistic model with lognormal observation error was the best fit relative to the exponential and Ricker models (as indicated by smaller AIC's). The fit of the mean only model was not significantly worse than the logistic model (using likelihood-ratio tests) for 11 of the 12 population types; the logistic was a significantly better fit for the remaining population (monoculture of 1312; $P = 0{\cdot}01$ d.f. = 2). There was a negative relationship (consistent with density dependence) between $N_{t+1} - N_t$ and N_t in all 12 populations used in this analysis (Table S1), and for eleven of these the slope was significantly different from zero. Tests for density dependence in time-series data are notoriously fraught with flaws (e.g. Freckleton *et al.* 2006). In particular, density dependence tests with time-series are subject to inflated type I error due to sampling error and/or incorrectly assuming that a population is closed. Some tests (e.g. Dennis & Taper 1994) may reduce this error, but a formal test using the Dennis and Taper approach would not be productive with these data because of the low power of that test using short time series such as these. In this experiment observation error should be minimal because populations were censused exhaustively, and preliminary data suggest the populations were closed (see above, N. Underwood, unpublished data). Because of the suggestion of density dependence in all populations and the better fit of the logistic than the mean only model, I focus here on analyses of the logistic model. Analyses of the mean only model yielded identical qualitative effects of variance in plant quality as the logistic (data not shown), so the conclusions of this study are not sensitive to using the logistic model over the mean only model.

I fit the logistic model with lognormal observation error to the data for each mono-, di- and triculture population type to obtain the best-fit parameters (r, K, and standard deviation) for each mixture and monoculture. Data from replicate populations of each type were fit simultaneously. Ninety-five per cent confidence limits for the best-fit parameters were generated by bootstrapping (Manly 1997), and likelihood-ratio tests comparing monocultures determined whether strawberry genotypes differed in aphid population dynamics. I calculated the expected parameters for aphids on each mixture as the average of the parameters (r and K) from the monocultures in that mixture. I used likelihood-ratio tests to determine whether the maximum-likelihood parameter estimates for each mixture differed significantly from the expected model [by comparing the model constraining both parameters to the additive expectation and the unconstrained (best-fit) model].

To address question 2 ('are the effects of variance negative or positive?'), I examined the relationship between the amount of variation in plant quality within a population and the deviation of aphid population size from the expectation using ANCOVA (Proc GLM, SAS). I modelled the deviation of the maximum likelihood estimate (MLE) of aphid K for a particular plant mixture from the expected K as a function of the variation in plant quality in that mixture [coefficient of variation of MLE K's from the monocultures of genotypes in that mixture, CV(K)], the genotype set of the mixture (A or B), and the interaction between CV(K) and set. I used untransformed values of the deviation; residuals did not deviate significantly from a normal distribution.

I explored the effect of the number of plant genotypes in a mixture on aphid population size (question 3; 'does plant genetic diversity affect aphid population size?') using repeated measures ANOVA (SAS, proc MIXED). Aphid population size on each population of six plants at each census was modelled as a function of the fixed effects spatial block, genotype set, and number of genotypes per population (including all populations), with mean plant size per population as a covariate and all two-way interactions. A 'Toeplitz' (banded) variance/covariance matrix was used, and residuals were approximately normal. When extinct populations were restarted, the extinction was counted as a zero population size, but otherwise re-started populations were considered a single trajectory. Dropping populations that went extinct did not change the qualitative results (results not shown). I also determined if strawberry genotypes differed in size by estimating the total leaf area in each monoculture and using one-way ANOVA to compare leaf areas among monocultures, and examined whether plant size differed between monocultures and mixtures using ANOVA (SAS, proc GLM) with plant size modelled as a function of block, genotype, monoculture vs. mixtures, and their interactions (the two genotype sets were examined separately).

Finally, to address question 4, ('how is aphid distribution related to variance in plant quality?'), I examined the distribution of aphids among plants within populations (summed over censuses and blocks) to determine whether the proportions of aphids on different plant genotypes in mixtures differed from the proportions expected if aphid populations on each plant grew independently (as in monocultures; question 4). I tested for differences between the distribution of aphids in mixtures and the expectation based on monocultures by using a likelihood-ratio test to compare a binomial model (multinomial for triculture populations) with equal distributions for monocultures and mixtures to one with different distributions for monocultures and mixtures. Alpha values were corrected using the Bonferroni method (Zar 1984). To summarize the pattern of differences in proportions of aphids on different genotypes between monocultures and mixtures, I calculated the difference in the proportion of aphids on the lowest quality plant genotype in a mixture (based on the MLE K for each genotype in monoculture) between the relevant monocultures and that mixture. For example, I calculated the difference between the proportion of aphids on genotype '55' in a diculture of '361' and '55,' and the proportion of the combined aphids on monocultures of '361' and '55' that were on the '55' monoculture. I determined whether the difference from the expected proportion of aphids on the low-quality genotype for each mixture was related to the difference between the expected and MLE values of K for that particular mixture using linear regression.

Results

NON-ADDITIVE EFFECTS OF PLANT GENETIC VARIATION ON APHID POPULATION DYNAMICS (QUESTIONS 1 AND 2)

Likelihood-ratio tests indicate that strawberry genotypes (monocultures) differed in aphid population dynamics, although genotypes within sets (A and B) did not always differ significantly (Table 1). Estimated carrying capacities varied by over two orders of magnitude, and rates of increase varied by an order of magnitude (Table 1). For some populations, estimated carrying capacities were similar to the starting density of the experiment; because these populations grew relatively little, estimates of the rate of increase have broader confidence intervals than estimates of carrying capacity

Table 1. Maximum-likelihood parameter estimates for the logistic model with lognormal observation errors fit to aphid populations on eight types of strawberry populations containing different genotypes of plants. Plant populations sharing letters in the last column did not differ significantly in the best-fit parameter estimates for their aphid populations

Set	Genotypes	*r* (95% CL)	*K* (95% CL)	SD (95% CL)	Monoculture comparisons
A	1312	1·15 (0·06–2·67)	5·40 (3·31–10·21)	1·23 (1·0–1·41)	A
A	34	1·09 (0·13–2·79)	6·55 (5·16–8·14)	0·65 (0·51–0·79)	A
A	W2	0·08 (0·03–2·40)	8·16 (5·89–14·62)	0·77 (0·56–0·93)	A
A	W2, 1312	0·16 (0·04–2·51)	11·83 (8·96–21·33)	0·78 (0·56–0·98)	
A	34, 1312	0·17 (0·08–2·35)	8·26 (5·59–13·19)	1·07 (0·8–1·28)	
A	34, W2	0·23 (0·13–2·59)	7·86 (5·81–10·34)	0·81 (0·57–0·99)	
A	34, W2, 1312	0·39 (0·12–2·58)	9·51 (5·78–10·42)	0·61 (0·57–0·99)	
B	D3	0·09 (0·05–1·0)	14·35 (11·04–18·26)	0·52 (0·37–0·58)	B
B	361	0·05 (0·04–0·1)	24·5 (10·8–33·3)	0·81 (0·57–0·94)	B
B	55	0·04 (.001–3·36)	0·19 (0·01–0·46)	0·43 (0·31–0·5)	C
B	D3, 55	1·33	3·96 (3·01–5·15)	0·65 (0·49–0·77)	
B	55, 361	2·64 (1–2·87)	4·52 (3·27–6·08)	0·77 (0·61–0·9)	
B	D3, 361	0·99 (0·99–1·05)	12·54 (8·9–17·5)	0·95 (0·75–1·13)	
B	D3, 55, 361	1·01	8·22 (6–30)	0·86 (0·57–1·07)	

Table 2. Test for non-additive effects of plant genotypes on aphid population dynamics. Likelihood-ratio tests compare the best-fit logistic model to one constrained to only additive effects for censuses of aphid populations on eight types of strawberry populations containing different mixtures of genotypes (where each observation is the number of aphids summed over six plants within a population). Both models use lognormal observation error and an unconstrained standard deviation. The constrained model fixed *r* and *K* at the values expected from the average of the MLE estimates from monocultures of the genotypes in that particular mixture.

Set	Genotypes in mixture	Likelihood ratio statistic (DF = 2)	*P* value
A	W2, 1312	13·9	0·001
A	34, W2, 1312	10·3	0·006
A	34, 1312	2·7	0·26
A	34, W2	0·29	0·86
B	D3, 55	10·81	0·004
B	55, 361	8·67	0·01
B	D3, 55, 361	0·28	0·88
B	D3, 361	0·13	0·94

(Table 1). The initial experimental aphid densities were set by the maximum feasible size of experimental plant populations in conjunction with the need to have initial aphids equally distributed over all plant genotypes. Natural densities of these aphids in the field are similar to or lower than the carrying capacities estimated in this experiment (N. Underwood, personal observation).

For aphid populations on four of the eight mixed-plant genotype populations, the best-fit logistic model was significantly different from the model with only additive effects (likelihood-ratio tests comparing the best-fit model for each mixture to a model constrained to the expected parameters for that mixture, Table 2). The same result was obtained using the density-independent mean only model (the same four populations showed significant deviations, all $P < 0{\cdot}01$; results not shown). The difference between the observed and expected (average of monoculture) population sizes at each census tended to be positive for mixtures in genotype set A and negative for mixtures in set B (Fig. 2) and the proportional difference between the observed and expected population sizes ranged from 0·07 to 0·74 (Fig. 3).

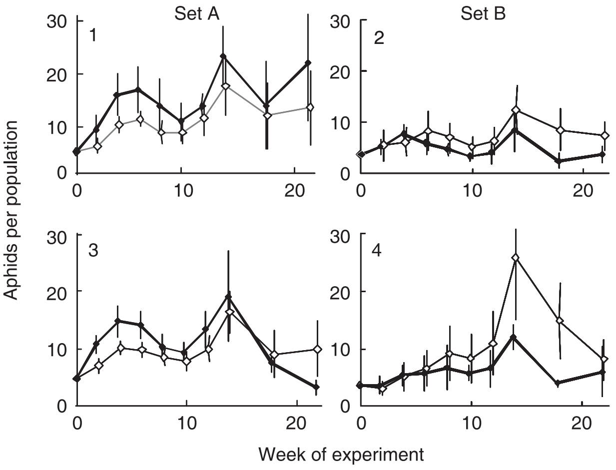

Fig. 2. Observed (filled symbols) aphid populations on plant populations that were mixtures of plant types. Open symbols show the average of aphid populations observed on monocultures of plant types in each mixture (not predictions from fitted models); these provide an approximate expectation for population sizes in the absence of an effect of variance. Four of the eight plant mixtures in the experiment are shown, two from plant genotype set A (panel 1, mixture of genotypes Wrights 2 and 1312; panel 3, mixture of Wrights 2, 1312, and 34) and two from plant genotype set B (panel 2, mixture of 55 and Doran 3; panel 4, mixture of 55 and 361). Points indicate average aphids per plant population at each census starting with release of experimental aphids at week zero and with each census increment being approximately 2 weeks; error bars indicate one standard error.

Across all mixtures, the amount of variation in plant quality in a particular mixture (coefficient of variation of MLE *K*'s for the monocultures involved in each mixture) had a marginally significant negative effect on the difference between the estimated equilibrium population size (MLE *K* for each mixture) and expected equilibrium population size (average

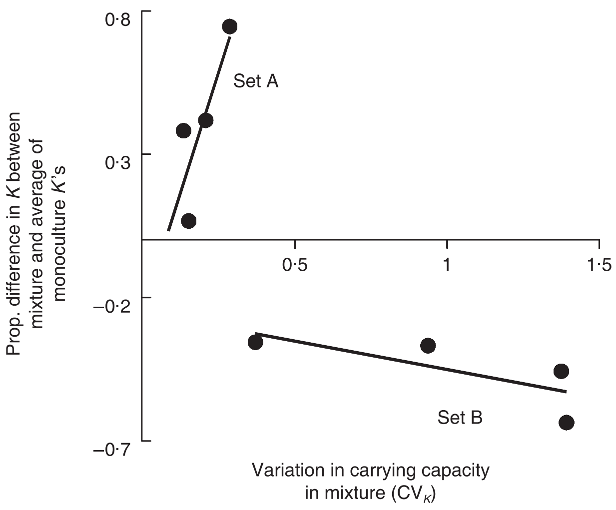

Fig. 3. Effect of variation in aphid carrying capacity across plants within a population of mixed plant genotypes on the proportional deviation of aphid population size at equilibrium (K) from the expectation if plant quality had only additive effects on aphid population size (average of aphid K's on monocultures of plant genotypes in the mixture). Variation in plant quality was measured as the coefficient of variation in carrying capacity, as estimated in monocultures of each plant type in a mixture. Each point indicates one particular mixture of plant genotypes.

of MLE K's from monocultures of genotypes involved in that mixture) (main effect of CVK_{monos} $F_{1,4} = 5·82$, $P = 0·07$). Interpretation of this effect is complicated by the fact that the sign of this relationship differed between plant sets (interaction of CVK with set, $F_{1,4} = 7·37$, $P = 0·05$), with a positive relationship across mixtures in set A, and a negative relationship across mixtures in set B (Fig. 3).

NUMBER OF PLANT GENOTYPES IN A POPULATION (QUESTION 3) AND PLANT SIZE

The number of genotypes in a plant population did not affect aphid population size (main effects of number of genotypes and interactions including number of genotypes all $P > 0·2$, Fig. 4). There was no significant effect of plant size on aphid population size. Plant size did not differ among monocultures (effect of plant monoculture genotype on plant size $P = 0·12$). There was a significant difference in plant size between the monocultures and mixtures in genotype set A only (interaction between monoculture vs. mixture and genotype, $F_{2,188} = 3·18$, $P = 0·04$) for only one of the three genotypes (genotype 1312, $P = 0.03$). Plants of 1312 were on average bigger in mixtures collectively, although there was no significant difference between monocultures and mixtures for any particular mixture. Because deviations from the expected population size in mixtures with genotype 1312 were positive (larger than expected population sizes), and genotype 1312 supported relatively low population sizes in monocultures this difference in plant size between monocultures and mixtures cannot explain the non-additive effects observed in this study.

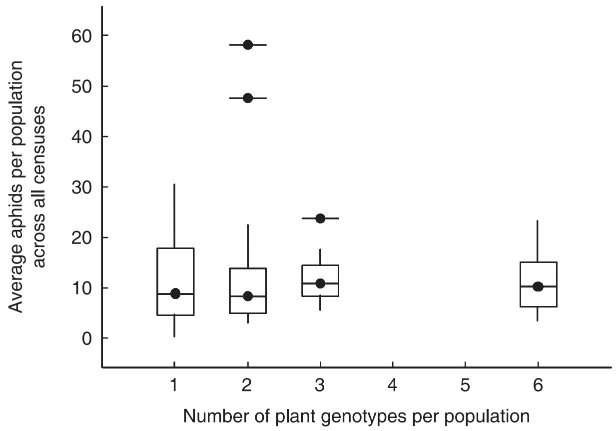

Fig. 4. Average size of aphid populations on plant populations with different numbers of plant genotypes. Dots in boxes indicate medians; boxes delineate the middle half of the data; whiskers extend to the most extreme non-outlier; and dots outside the boxes indicate outliers. $N = 9$ for each box.

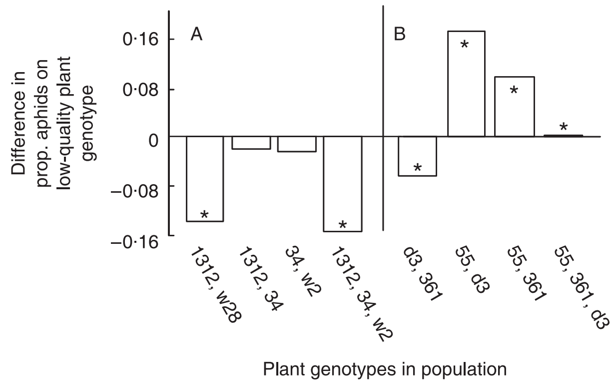

Fig. 5. Difference between the proportion of aphids on the lowest-quality plant genotype in each mixed plant population and the proportion of aphids on that genotype in monocultures. Asterisks indicate significant differences, $P < 0·006$. Each bar represents either five (for set A) or four (for set B) replicate populations of each mixture. Aphids on each genotype in each population were summed over all censuses.

DISTRIBUTION OF APHIDS AMONG PLANTS WITHIN MIXED PLANT POPULATIONS (QUESTION 4)

For most mixtures, the proportion of aphids on the lowest-quality strawberry genotype differed significantly from the proportion on that genotype in the monocultures (likelihood-ratio tests, Fig. 5). For plant genotype set A, these differences were all negative (fewer aphids were found on low-quality genotypes in the mixtures than in monocultures), whereas for set B, differences tended to be positive (more aphids were found on low-quality genotypes in the mixtures). The difference in the proportion of aphids on the low-quality plants between the monocultures and the mixtures was significantly related to the difference between the expected (average) K's and the best estimates of K for each mixture (regression,

$F_{1,6} = 8{\cdot}8$, $r^2 = 0{\cdot}59$, $P = 0{\cdot}025$); mixtures with larger proportions of aphids on lower-quality genotypes showed more negative deviations of their MLE K from the expected K.

Discussion

Theory suggests that the equilibrium sizes of populations inhabiting collections of habitat patches of differing quality should be influenced not just by average patch quality (additive effects) but also by variance in patch quality (non-additive effects) due to a range of possible mechanisms (Bernays 1999; Ruel & Ayres 1999; Underwood 2004). Results of the present study show that genetic variation in quality within strawberry plant populations can influence strawberry-aphid population size in the field. For half of the strawberry genotype mixtures in this experiment, the best-fit models summarizing aphid population dynamics differed significantly from models assuming only additive effects of each plant genotype on aphid population size (Table 1, Figs 3 and 4). These results were the same regardless of whether population growth was modelled using the density-dependent logistic, or density-independent 'mean only' model.

One mechanism that might contribute to the observed effects of variance in plant quality on aphid populations is a source-sink dynamic between high- and low-quality plants (Underwood 2004), where 'source' plants would have growing aphid populations and 'sink' plants would have shrinking aphid populations (Pulliam 1988). Whether the effect of variance in habitat quality due to source-sink dynamics is positive or negative depends on the correlation between rate of increase and density dependence across patches within a population (Underwood 2004). Positive correlations between r and K can, over some levels of variance, produce positive deviations from expected population size, while negative correlations produce negative deviations. The results of the present study are qualitatively consistent with source-sink dynamics. Larger amounts of variance in plant quality were associated with larger deviations of aphid population size from the additive expectation, and both positive and negative effects of variance were observed depending on plant genotype set (Fig. 3). No significant correlation between r and K was detected for either genotype set (Underwood 2007), but because each set included only three plant genotypes, the power to detect any correlation was low. Estimates of r were also less certain than estimates of K (Table 1). Therefore, although plant genotype sets differed in the effects of variance on aphid population size, it cannot be determined whether correlations between r and K contributed to this difference. The source-sink mechanism requires aphid movement among plants, which was directly observed in this experiment, and can also be inferred from the fact that mixtures (where aphids could move among plants) and the relevant monocultures (where aphid populations grew independently) generally differed significantly in the proportion of aphids on each plant genotype. The source-sink mechanism also requires density-dependent population growth; there is weak evidence for density dependence from this experiment (Table S1).

Jensen's inequality suggests that the observed non-additive effects might also arise from a nonlinear relationship between plant quality and herbivore population size (Ruel & Ayres 1999). This mechanism would be consistent with the observed increasing deviations from additivity with increasing variance, and could account for the change in direction of deviations between genotype sets if the relationship between plant quality and herbivore population growth changed from concave to convex between genotype sets (Miller 2007). It is not possible to evaluate the contribution of nonlinearities to the data reported here because the relationship between plant quality traits and aphid population size is unknown.

Several other mechanisms could also contribute to an effect of variance in plant quality on herbivore population dynamics. Negative effects of variation in plant quality might arise directly through a reduction in herbivore performance because of a variable diet (Stockhoff 1993) or indirectly through increased herbivore movement in variable environments (Bernays 1999) resulting in less feeding time and greater exposure to predators. Positive effects could arise if herbivores were able to choose higher- over lower-quality plants. Preliminary data suggest that strawberry aphids do not suffer reductions in fecundity when switched among plant genotypes during development (S. Halpern and N. Underwood, unpublished data), but that the rate of aphid movement among plants can differ between plant genotypes, with mixtures of plant genotypes producing greater aphid movement than monocultures (N. Underwood, unpublished data). Further work is needed to determine how these mechanisms might contribute to the effect of variance in plant quality reported here.

All the mechanisms discussed above require herbivore movement among plants; at least two additional mechanisms could operate without among-plant movement. First, the identity of neighbouring plants could affect individual plant quality. If competition were stronger between more similar plants (Schmitt & Antonovics 1986), plant quality could be lower in low- than in high-variance plant mixtures (assuming similarity of quality scales with relatedness). Second, according to the 'enemies' hypothesis (Root 1973), mixtures of plant species might support larger predator populations than monocultures by providing greater variety of resources (alternative prey or nectar) for predators. I have no evidence that either of these mechanisms was operating in the present experiment. Later experiments in the same plant populations used here (data not shown) indicate that the effect of a strawberry genotype on aphid population growth does not differ between aphids caged on individual plants in monocultures (with same-genotype plants as neighbours) and mixtures (with neighbours of different genotypes). Because I did not observe parasitized aphids in these populations, and other predators were very rare, there is no way of estimating possible predator effects. Although plant quality as hosts for aphids clearly affected aphid populations, the strawberry genotypes did not differ enough in morphology or blooming season that mixtures offered noticeable increases in predator microhabitats or floral resources over monocultures.

A large body of mostly agricultural literature addresses how the number of plant types (species or varieties) affects herbivore population size within a field (reviewed in Andow 1991). I found no evidence that the number of strawberry genotypes in a population influences aphid population dynamics. Populations of aphids on plant populations with two, three, and six genotypes were on average no smaller or larger than populations on monocultures (Fig. 4). This result is consistent with many agricultural studies of mono- and polycultures that found no effect (Andow 1991) and contrary to other studies that do find an effect of number of genotypes on insect abundance (Andow 1991; Crawford *et al.* 2007). This variety of outcomes is not necessarily surprising. Interest in using polyculture to control pests stems from the idea that plant mixtures might have non-additive effects on herbivores. However, populations with equal numbers of plant types can have very different levels of variance in plant traits, depending on the particular plant types present in each mixture, so manipulating number of plant types is a poor test for effects of variance (or non-additivity). As a practical method for pest control, results of the present study suggest that polyculture can be effective in lowering herbivore population sizes, but that individual polycultures would need to be evaluated on a case-by-case basis to determine their effectiveness.

Summary

Populations of mobile herbivorous insects frequently occupy collections of plant 'patches' that differ in quality as food because of differences in species, genotype, or phenotype. My results suggest that variation in plant quality can affect herbivore populations non-additively. Predicting the behaviour of herbivore populations from knowledge of average plant quality may therefore not be possible. Considerable interest has focused on using plant diversity to manage herbivore populations in agriculture. Results of the present study suggest that polycultures might lower herbivore population sizes, but that we cannot expect all polycultures to do so. The non-additive effects I observed of plant quality on herbivore population distributions among plant genotypes also suggest that variance in plant quality can influence the herbivore loads of individual plants, resulting in either associational resistance (Tahvanainen & Root 1972) or susceptibility depending on whether effects are negative or positive. Variance among plants might therefore also contribute to the dynamics of the evolution of resistance in plant populations (Tiffin *et al.* 2006). Finally, the dynamics of any population will depend on both its environment and on the population's own genetic composition (Hanski & Saccheri 2006). Fully understanding the dynamics of herbivore populations may require a framework that includes both variation among host plants and how that variation interacts with herbivore genetic composition.

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Supporting Information

The following supporting information is available for this article online

Table S1. Regressions of the change in aphid population size from census t to $t + 1$ against the population size in at census t for each plant population type. Negative relationships suggest density dependence. N for each test = 9. P values are presented for reference but should be interpreted with caution due to a likelihood of inflated type I error.