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Sources of Variation in Insect Density on *Lupinus arboreus* Sims: Effects of Environment, Source Population and Plant Genotype

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ABSTRACT.—Temporal and spatial variability in herbivory can be influenced by plant genotype, environmental conditions and their interactions. However, few studies correctly control for the relative influence of these factors. Here, I report results from a reciprocal common garden experiment designed to tease apart the effect of local environmental variation and plant genotype on the abundance of four insect species: *Dasineura lupini* (Felt), *D. lupinorum* (Gagne), *Epinotia infuscana* (Walsingham) and *Orgyia vetusta* (Boisduval). Full-sib/half-sib families of *Lupinus arboreus* Sims were made within three different natal populations; replicates from each lupine family then were transplanted back into common gardens located in each of the three parental populations. In two separate years I measured how insect density varied between local environments, within a population of related lupine and among the three populations of lupine. For each insect species, local environment influenced density substantially and microsite variation within environments explained a significant amount of variation. Two insect species (*E. infuscana* and *O. vetusta*) congregated on plants originating from the same parental population more than lupine from other populations, while the other two insect species showed this pattern only in specific environments. Even though these insects were differentially abundant on lupine from the three natal populations, they rarely discriminated among individual genotypes within a population. Thus, insect density was affected by environmental factors unique to each site and partly by genotypes originating from the same natal origin, but rarely by fine-scale differences among genotypes from within one parental population.

INTRODUCTION

The environment that sessile plants inhabit can change dramatically across relatively short geographic distances (Antonovics and Bradshaw, 1970; Snaydon and Davies, 1982; Linhart and Grant, 1996). Spatially varying selection imposed by herbivory or by heterogeneity in environmental factors may be responsible for genetic variation in plant life history traits (Bradshaw, 1972; Jules and Shaw, 1994; Kalisz *et al.*, 2001; Kittelson and Maron, 2001) and in plant resistance to insect herbivory (Louda, 1982).

Genetic differentiation in plant traits may mean that genotypes vary in insect suitability, susceptibility or the amount of damage they are likely to suffer (Maddox and Root, 1987; Karban, 1992; Marquis, 1992; Zangerl and Berenbaum, 1997; Horner and Abrahamson, 1999). Genetic variability for the production of secondary defense chemicals (*e.g.*, alkaloids) also may influence insect damage (Mankinen *et al.*, 1975; Harrison and Karban, 1986; Adler and Kittelson 2004). As a result, insect damage may be localized to specific individuals within a population or among populations comprised of related genotypes (Karban and Kittelson, 1999).

Variation in environmental conditions also can result in some populations being more suitable for insect growth, survival and reproduction (Maddox and Cappucino, 1986;

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Collinge and Louda, 1988; Stiling and Rossi, 1995). However, it is often unclear if spatial variation in herbivory is due to genetic differences among host plants and/or environmental variability. Many experiments that correlate insect damage to plant traits or to environmental variables fail to control for the relative influence of environment vs. plant genotype (except *see* Rossi and Stiling, 1998; Stiling and Rossi, 1995, 1996; Graham *et al.*, 2001). Reciprocal common garden experiments conducted with plants of known parentage are a powerful way to isolate how herbivory is affected by genotype, environmental conditions and gene by environment interactions.

At the study site along the California coast, *Lupinus arboreus* Sims occupies two environments (grasslands and dunes) that sharply abut each other along the San Andreas Fault. Grassland and dune environments differ in soil organic content, phosphorus, nitrogen and water availability (Bodega Marine Reserve, unpubl.). Populations of *L. arboreus* also experience spatial and temporal variability in plant cover and herbivory; damage to individual plants and among lupine populations can vary dramatically. For example, in some grassland populations lupine cover can fluctuate between <5% and 75% (Strong *et al.*, 1995; pers. obs.). At these sites, plants recruit episodically, grow at high density, but frequently die from heavy insect herbivory (Strong *et al.*, 1995; Maron, 1998). However, at other sites lupine populations are more stable despite herbivory by other insects (Harrison and Maron, 1995). Insect diversity also varies among sites (Maron *et al.*, 2001; pers. obs.). Finally, lupine life-history traits are genetically based and correlated with specific populations; in common gardens, genotypes from the same natal population have similar canopy size, flowering time, seed set and mortality, whereas lupine originating from another population express these traits differently (Kittelson and Maron, 2001). These unique patterns in plant life-history traits may affect insect abundance or level of damage. For example, genotypes that are larger and set more seed (Kittelson and Maron, 2001) may attract higher densities of insects.

In this experiment, variation in plant phenotype caused by the environment was controlled with a reciprocal common garden design, and the densities of four insect species on related lupine genotypes were measured in two consecutive years. I analyzed how insect density varied within and among three environments, among plants from different natal populations and within paternal or maternal families. From these results, I addressed if insects respond to fine-scale differences among individuals and among populations of related genotypes or if, in a common environment, they simply attack plants regardless of genotype.

METHODS

Study organism and site.—Yellow Bush Lupine, *Lupinus arboreus* (Fabaceae), is a nitrogen-fixing, perennial shrub common to northern California's coastal prairie and dunes (Hickman, 1993). At the study site, located in the Bodega Marine Reserve (BMR) in Sonoma County, California, *L. arboreus* is abundant in adjacent grassland and dune habitats. Lupine seedlings emerge during the rainy season from December to March and grow rapidly within one season (Davidson and Barbour, 1977). Most shrubs flower in their second spring and seeds disperse explosively in late summer. Bush lupine at this site have a mixed mating system, with an outcrossing rate of 0.78 (Kittelson and Maron, 2000).

The three populations used in the current study were located at Bayshore (BS) and Mussel Point (MP), which are grassland sites, and in the Dunes (DUN; Fig. 1). Within this system, herbivory on individual plants and among the populations varies (Harrison and Maron, 1995; Strong *et al.*, 1995; Karban and Kittelson 1999). At BS, cover and persistence of bushes is highly variable, with average lupine cover fluctuating from 0% to 60% over 10 y periods (Strong *et al.*, 1995). Fluctuations in cover may be caused by high rates of herbivore

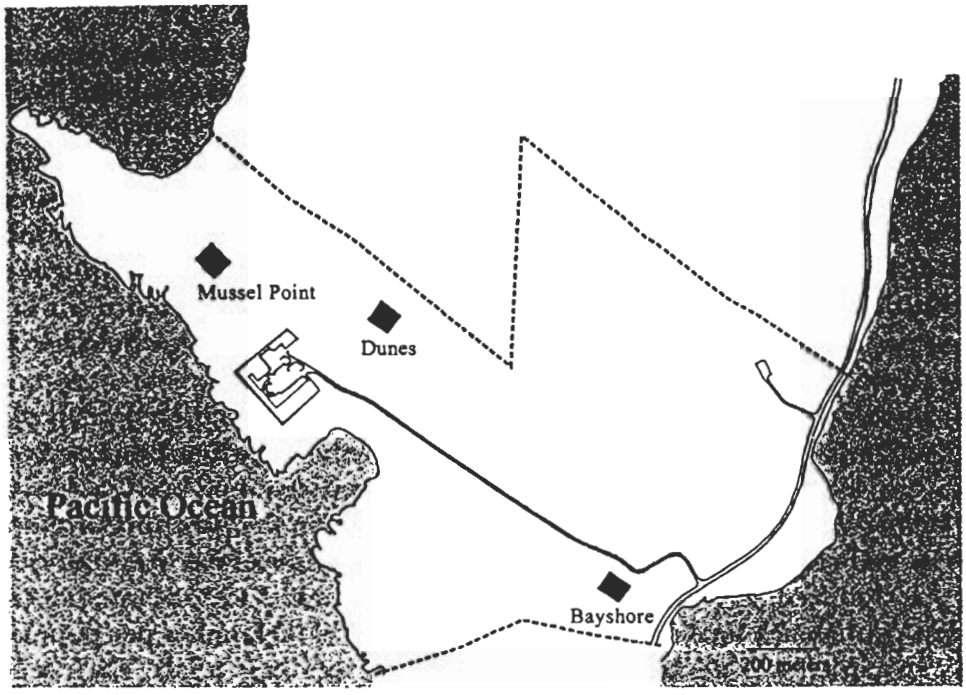

FIG. 1.—Map of the Bodega Marine Laboratory and Reserve illustrating the locations of three lupine stands: Bayshore (BS), Dunes (DUN) and Mussel Point (MP). Stippled boundaries delineate the Reserve property. Solid boxes indicate the relative location of common gardens. Half-sib, full-sib families were made in areas adjacent to the common gardens

damage due, in part, to the subterranean caterpillar, *Hepialus californicus*, and the folivorous California tussock moth, *Orgyia vetusta* (Strong *et al.*, 1995; Maron, 1998; Maron and Harrison, 1997; Preisser, 2003). Lupine from BS origins grew quickly, set copious seed in the second year and experienced low mortality in a reciprocal common garden experiment (Kittelson and Maron, 2001). At MP, lupine cover is more extensive than at the other two sites, between 45%–75% cover, and does not fluctuate dramatically despite heavy herbivory of adult and seedling lupine by *Orgyia vetusta* (Harrison and Maron, 1995; Maron, 1997). In common gardens, plants from MP families were generally smaller, produced few seeds and had the highest mortality compared to lupine from other populations (Kittelson and Maron, 2001). At DUN, lupine cover is sparse relative to grassland sites, but is relatively stable (cover ranges from 20% to 45%), and insect herbivory is only moderate and rarely causes stand die-off. In common gardens, lupine from DUN families were intermediate in size, seed-set and mortality relative to plants from the other two populations (Kittelson and Maron, 2001).

Insects representing several guilds feed upon *Lupinus arboreus* roots, leaves, flowers and seeds (Kittelson, 1998). Additionally, mammals such as deer and rodents negatively affect lupine either by direct removal of above-ground tissue, seed predation or by burrowing (Kittelson, 1998; Maron and Simms, 1997, 2001). This experiment focused on four insect species: two galling Cecidomyiid Dipterans, *Dasineura lupini* (Felt) and *D. lupinorum* (Gagne), a Tortricid Lepidopteran that bores into the apical meristem, *Epinotia infuscana* (Walsingham), and a Lymantiid Lepidopteran folivore, *Orgyia vetusta* (Boisduval).

Creation of full-sib and half-sib families.—To examine both genetic and environmental influences on insect abundance among subpopulations of *Lupinus arboreus*, full- and half-sib families were created within each of the three sites (MP, DUN and BS). In April 1995, six

randomly selected pollen-donating plants (sires) were crossed with five seed-producing plants (dams) within each of the three populations. I conducted crosses in a complete 6 × 5 factorial design. This resulted in a total of 30 full-sib, and six paternal and five maternal half-sib families from within each population.

The crossing design ensured that all seeds from the same fruit and inflorescence were full-siblings, those from different inflorescences on the same dam were maternal half-siblings and those from different bushes that were pollinated from the same sire were paternal half-sibs. The complete methodology for crossing and controlling *Lupinus arboreus* pollinations is described in Kittelson and Maron (2000, 2001). Collected seeds were stored at room temperature for 4 mo. Plant families were grown in common gardens located within each natal population.

Common gardens.—In spring 1995, I established 20 m × 20 m common garden plots within the three lupine populations at MP, DUN and BS. Common garden plots were cleared of existing shrubs; all vegetation, with the exception of lupine, was allowed to re-establish. In February 1996, 3-wk old seedlings, which had been grown in the greenhouse, were planted randomly in each common garden. Each garden was divided into three blocks and two randomly selected seedlings from each of the 90 full-sib families were planted in each block. Each garden contained a total of six seedlings from each of 90 families per population (540 seedlings per garden × 3 destination gardens = 1620 seedlings total). Each seedling was marked with a flag and a numbered identification tag. During weekly inspections in spring, lupine seedlings that had germinated naturally from the seed bank were manually removed from each garden. After planting assemblages of relatives from the three populations in reciprocal common gardens, I determined the relative effects of plant genotype, environmental variation and/or gene by environment interactions on insect densities.

Trait measurements.—In August 1996 and 1997, plant height, maximum crown diameter and a second crown diameter taken at a right angle to the maximum were recorded and used to calculate plant size (height × the two canopy diameters). To control for plant size, densities of insects were recorded in the following ways: the average number of *Dasineura lupini* and *D. lupinorum* galls from four 10 cm^3 quadrats; the average number of five randomly selected shoot tips infected with *Epinotia infuscana* and the number of *Orgyia vetusta* caterpillars counted in four 25 cm^3 quadrats. Insect populations were sampled when densities were maximum.

Statistical analyses.—The relative effects of genetic and environmental differences on insect herbivores and plant traits were assessed using a Multiple Analysis of Variance (proc MANOVA; SAS Institute, 1990). Density of each insect species was related to common garden (site), natal seed origin (which were treated as fixed effects), block, maternal and paternal identity (which were treated as random effects) as well as their interactions. To meet the assumptions of the MANOVA, all insect densities were transformed [sqrt (n + 5)]. When overall MANOVA results were significant (*see* Results), effects of independent variables on each insect species' density were further investigated using a mixed model ANOVA (PROC GLM; SAS Institute, 1990). Log of plant size was used as a covariate in all analyses of insect abundance to control for the effect of plant size on insect choice. Plants dying between planting and census in 1996 or between 1996 and 1997 were deleted since no data could be collected for them. Separate statistical analyses were performed for each year because 193 plants died between years and three out of four insect species did not occur in sufficient densities in both years (*see* Results). Proper error terms were determined using the random statement and 'test' option (SAS Institute, 1990).

Within these models, a significant destination effect indicates that the common garden environment (*i.e.*, destination site) alters herbivore densities. Significant origin effects indicate that genetic or maternal environmental factors vary among natal populations and

influence herbivores. Paternal effects indicate that additive genetic variance influences herbivore abundance and damage, while maternal effects indicate significant genetic and maternal environmental affect on herbivores. A significant site-by-origin interaction is similar to a genotype-by-environment interaction where the relative rank of genotypes supporting certain insect densities changes significantly across the common garden environments and provides evidence for origin-specific differentiation in response to site.

In addition to analyzing variation in traits across all sites, I was also interested in decomposing the sources of variation in traits *within* each garden; this was done by analyzing each site independently with separate MANOVAs for each common garden. When overall MANOVA results were significant, I report effects of dependent variables on each trait in isolation using a mixed model ANOVA. In these analyses, the effects of origin, block, maternal and paternal families and their interactions on insect density were determined. Data are reported for these independent, *within* garden analyses only if they showed different patterns relative to analyses *across* the reserve, and are only reported in the text.

Partial correlations also were determined from covariance matrices to examine the relationship between seed origin, plant size, mortality and/or seed production to overall insect abundance (PROC GLM, SAS Institute, 1990).

RESULTS

The combined densities of insects from 1996 and 1997 were significantly different across BMR and were dependent on origin, destination site, maternal and other model factors (MANOVA, Table 1). Therefore, I report effects of dependent variables on each insect species using individual ANOVAs. Across BMR, density of each insect species was influenced strongly by environmental factors in the destination garden (Table 2), so each destination garden also was analyzed independently and values for these within garden analyses are reported in the text.

Sources of variation in insect density during 1996.—There were significant effects of environment and natal seed origin on density of *Epinotia infuscana* (Table 2). Lupine from both grassland populations had on average two to three times more *E. infuscana* larvae than DUN families, especially when lupine were planted in the grassland destination gardens (Fig. 2). The DUN site, as well as DUN plant families, supported fewer larvae. The number of *E. infuscana* was highly correlated with plant size ($r = 0.49$, $df = 1068$, $P < 0.001$); not surprisingly, larger plants supported more larvae. *Epinotia infuscana* also induced changes in plant architecture. The number of larvae present in shoot apices before the plants began branching was related to the number of branches that were produced 2 mo later; plants with no larvae in their apices produced fewer branches than plants with two to five larvae (Pearson's $r = 0.71$, $df = 1068$, $P < 0.001$).

The number of bud galls (*Dasineura lupini*) on juvenile plants varied significantly depending on destination environment, within-site heterogeneity and the interaction of the destination site with both maternal and paternal families (Table 2). Interaction of the destination site with both maternal and paternal families was explained by the within-site analyses; at MP, insect densities were significantly influenced by lupine seed origin ($MS = 13.4$, $F_{2, 15} = 4.20$, $P < 0.001$) and maternal ($MS = 5.26$, $F_{12, 61} = 2.88$, $P = 0.004$) and paternal families ($MS = 3.32$, $F_{15, 60} = 1.82$, $P = 0.03$). Within the MP garden, plants from the BS seed origin had between 35% and 45% more bud galls on average than plant families from either the DUN or MP. Plant genotype did not explain insect densities within either the DUN or BS gardens.

Leaf galler (*Dasineura lupinorum*) density was significantly affected by environment including microsite variation and the interaction between destination site and seed origin

TABLE 1.—Multivariate analysis of variance (MANOVA) performed on density of three species in 1996 and two insect species in 1997. Analyses examine the effects of destination garden, seed origin (all fixed effects), block and maternal and paternal identity (all random effects) and their interactions (SAS Institute 1990). To meet the assumptions of the MANOVA, insect densities were transformed [sqrt (n+5)]

Source of variation	Wilks' Lambda	F	df	P
A. Insects in 1996				
Destination site	0.593	79.6	8	<0.0001
Seed origin	0.948	7.24	8	<0.0001
Block	0.932	3.16	24	<0.0001
Maternal family (origin)	0.919	1.90	48	0.0002
Paternal family (origin)	0.927	1.36	60	0.035
Maternal * paternal (origin)	0.820	0.90	240	0.857
Site * origin	0.936	4.44	16	<0.0001
Site * maternal (origin)	0.891	1.30	96	0.028
Site * paternal (origin)	0.876	1.20	120	0.075
Site * maternal * paternal (origin)	0.675	0.92	480	0.889
B. Insects in 1997				
Destination site	0.410	122.50	8	<0.0001
Seed origin	0.910	10.55	8	<0.0001
Block	0.685	14.53	24	<0.0001
Maternal family (origin)	0.894	2.06	48	<0.0001
Paternal family (origin)	0.919	1.24	60	0.103
Maternal * paternal (origin)	0.761	1.03	240	0.370
Site * origin	0.923	4.50	16	<0.0001
Site * maternal (origin)	0.830	1.73	96	<0.0001
Site * paternal (origin)	0.866	1.07	120	0.296
Site * maternal * paternal (origin)	0.579	1.07	480	0.171

(Table 2). Plant size also affected the densities of galls, with greater densities on larger plants. Within both the MP and BS gardens, the seed origin of lupine strongly affected densities of *D. lupinorum* ($MS=16.7, F_{2,10}=3.37, P<0.001$; $MS=307, F_{2,7}=11.5, P<0.001$, respectively). In both of these grassland destination gardens, lupine families from BS had between 70% and 100% more leaf galls than lupine families originating from MP or DUN, respectively. Seed origin did not affect density of *D. lupinorum* at the DUN destination garden.

Sources of variation in insect density during 1997.—Densities of bud and leaf gallers in 1997 were not analyzed because so few were recorded (12 lupine of 875 supported *Dasineura lupini* and only 27 lupine of 875 had *D. lupinorum*). However, plants were affected by *Epinotia infuscana* larvae and one folivore species, *Orgyia vetusta*, previously not recorded.

Densities of *Epinotia infuscana* were explained by environment (destination site and block) and by natal seed origin (Table 2). Density was affected by the size of the plant (Table 2); bigger plants supported more larvae on a per area basis. At all gardens, DUN families supported fewer larvae than did plants from the two grassland sites.

Orgyia vetusta were recorded only at the BS garden. Origin, heterogeneity within the garden, maternal parent and size of the plant explained the variation in damage by *O. vetusta* (Table 3). Lupine families originating from BS sustained higher densities of *O. vetusta* (Fig. 3).

Correlations.—Overall, regardless of destination garden, lupine families originating from the BS population supported more insects when compared to plants from the other two seed origins. There was a strong relationship between BS families and overall insect density

TABLE 2.—General linear model results among all gardens for the density of four insects: *Epinotia infuscana* in 1996 and 1997, *Dasineura lupini* and *D. lupinorum*. Dead plants were excluded from the analyses. Error degrees of freedom were 875 for *Epinotia infuscana* in 1997. Mean square and F values are type III sum of the squares, * denotes a $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$

	Epinotia infuscana in 1996			*Dasineura lupini* in 1996	
Source	df	MS	F	MS	F
Destination site	2	18.7	58.1***	50.9	25.5***
Seed origin	2	8.55	19.8***	3.01	0.78
Block	6	0.69	1.10	2.50	2.52*
Maternal family (origin)	12	0.65	1.06	3.40	2.12
Paternal family (origin)	15	0.44	0.99	1.56	1.15
Maternal * paternal (origin)	60	0.68	1.14	0.85	1.05
Site * origin	4	0.24	0.80	2.34	1.14
Site * maternal (origin)	24	0.53	0.90	1.57	1.94*
Site * paternal (origin)	30	0.36	0.60	1.32	1.62*
Site *maternal *paternal (origin)	120	0.59	0.94	0.81	0.81
Canopy size	1	77.1	123***	0.47	0.47
Error	1068	0.63		0.99	
	Dasineura lupinorum in 1996			*Epinotia infuscana* in 1997	
	df	MS	F	MS	F
Destination site	2	2092	56.0***	124	130***
Seed origin	2	184	3.47	26	12.1**
Block	6	93	5.00***	16	17.7***
Maternal family (origin)	12	45	1.43	1.95	2.28
Paternal family (origin)	15	30	1.25	1.20	1.23
Maternal * paternal (origin)	60	20	0.88	0.96	0.92
Site * origin	4	133	3.44*	1.24	1.28
Site * maternal (origin)	24	35	1.55	0.95	0.90
Site * paternal (origin)	30	27	1.20	1.07	1.02
Site * maternal * paternal (origin)	120	22	1.2	1.06	1.19
Canopy size	1	1325	71.3***	16.9	18.9***
Error	1068	18.6		0.89	

($r = 0.648$, $df = 420$, $P < 0.001$); families derived from the other two sites of origin supported far fewer insects overall ($r = 0.143$, $df = 401$, $P = 0.12$ and $r = 0.079$, $df = 352$, $P = 0.20$ for DUN and MP families, respectively).

Total insect density was not significantly correlated to mortality ($r = 0.217$, $df = 985$, $P = 0.112$) or seed production ($r = 0.122$, $df = 985$, $P = 0.341$) in 1997; however, larger plants tended to sustain greater densities of insects ($r = 0.583$, $df = 985$, $P < 0.001$).

DISCUSSION

Insect density varied temporally and spatially at BMR. Of the four species of insects, only *Epinotia infuscana* were present at significant densities on lupine in both years, while the galling insects (*Dasineura* spp.) were present only in 1996, and *Orgyia vetusta* consumed lupine only in 1997. Densities of all four species responded strongly to variation in environmental factors and led to greater insect density in some destination sites relative to others, especially the BS destination garden. Environmental factors likely changed across

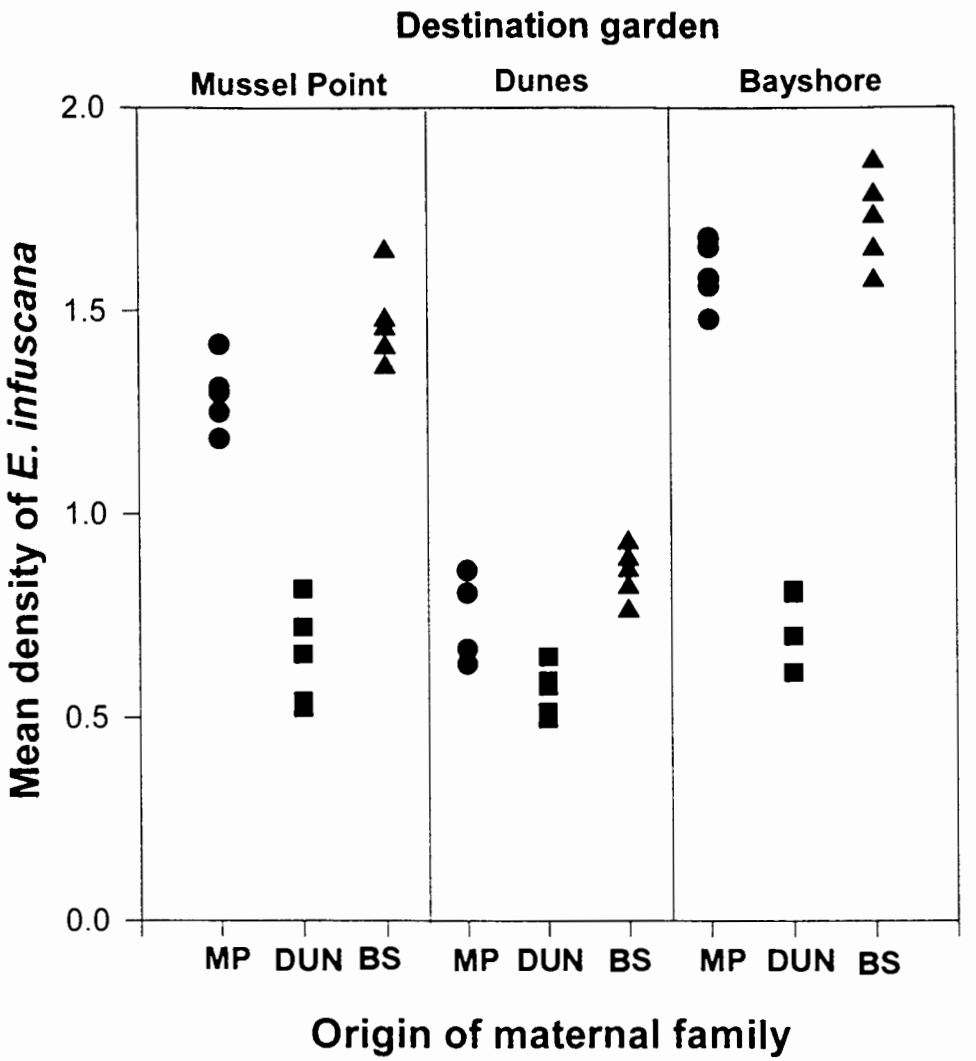

FIG. 2.—Mean number of apical borers (*Epinotia infuscana*) in 1996 for each maternal half-sib family of *Lupinus arboreus* in each of the three common gardens

relatively short distances because blocks within sites also affected insect densities for *E. infuscana* in 1997, *O. vetusta* and the galling insects.

Variation in insect density among and within gardens suggested that one destination site, BS, was most amenable to insect survival and persistence. The BS garden harbored the highest densities of all insects in both years and *Orgyia vetusta* was detected only at this destination garden. Densities of many insect species are affected significantly by environmental conditions (Louda, 1983; Stiling and Rossi, 1995). Variation in nutrient availability (Bryant *et al.*, 1993), light level (Collinge and Louda, 1988; Rossi and Stiling, 1998) and the absence of parasitoids or predators (Stiling and Rossi, 1996; Stiling and Bowdish, 2000) have been found to influence the abundance of herbivorous insects. However, for *O. vetusta* at BMR, Harrison (1997) found that neither host quality, predator abundance nor rates of predation explained the location of outbreaks. Rather, poor dispersal ability was the only consistent explanation for *O. vetusta's* limited distribution at BMR. In the current study, *O. vetusta* also was localized to BS. Moreover, density varied within blocks, which suggests that the folivore may prefer or is restricted to specific microsites within this broader area.

Table 3.—Analysis of variance for number of *Orgyia vetusta* per plant for *Lupinus arboreus* in 1997 in the Bayshore garden. No *O. vetusta* were found in the Dunes or Mussel Point garden. Plant size used as a covariate. Mean square and F values are type III sum of the squares. * denotes $P < 0.05$, ** denotes $P < 0.01$, and *** denotes $P < 0.001$

Source	df	MS	F
BAYSHORE			
Block	2	2.64	3.30*
Origin	2	27.4	34.2***
Maternal family (origin)	12	2.23	2.79***
Paternal family (origin)	15	0.69	0.86
Maternal * Paternal (origin)	60	0.80	1.01
Log of Plant Size	1	164	205***
Error	447	0.79	

The remaining three insect species in this study (*Dasineura* spp. and *Epinotia infuscana*) developed inside lupine; thus, environmental effects likely were mediated through lupine quality. Gall-forming insects are strongly influenced by host plant quality (Amwack and Leather, 2002; Weis *et al.*, 1988), and host plant quality can be affected by shading (Rossi and Stiling, 1998), nutrient levels (Bryant *et al.*, 1993) and environmental stress (Collinge and Louda, 1992). The BS destination garden may be a very stressful environment for lupine because all families had the lowest fitness in this garden relative to the other two destination gardens (Kittelson and Maron, 2001). The current experiment showed that insect densities were highest at BS suggesting that abiotic conditions at the BS destination garden may decrease lupine resistance or make them more attractive to insect herbivores. Interestingly, while leaf alkaloids in plants from all natal origins were highest at BS, *E. infuscana* and the bud gallers were not significantly affected by total alkaloids or alkaloid composition (Adler and Kittelson, 2004).

Within each destination site, *Epinotia infuscana* and *Orgyia vetusta* were more abundant on lupine from the same natal population relative to plants from other seed origins; insects preferred plants originating from BS. However, insects rarely made fine-scale choices among plants originating from within the same population. For example, *E. infuscana* and *Dasineura lupinorum* preferred BS plants, but they did not differentiate among individual genotypes within that population. Only *O. vetusta* and *D. lupini* at MP appeared to make distinctions among families. Failure to detect consistent family effects could be a result of small sample sizes resulting in lower statistical power. For example, the total number of maternal and paternal half-sib families created in each natal population was relatively low for confidently detecting paternal effects. Also, lupine growing at BS and DUN suffered considerably more mortality than plants at MP; consequently, there were fewer representatives to test the effect of family identity on herbivore density.

The significant effect of natal seed origin on insect density suggests that insects congregate on a group of related plants from the same population. For example, in all years and sites, *Epinotia infuscana* tended to prefer lupine that originated from the two grassland populations. Additionally, both species of *Dasineura* and *Orgyia vetusta* were more abundant on lupine families originating from BS. DUN families had the fewest *E. infuscana* and low densities of the other insect species suggesting that these families may possess genetic resistance.

Most of the insects in this study were not affected by fine-grained differences among genotypes from within a population. Only *Orgyia vetusta* and *Dasineura lupini* at MP differentiated among specific maternal or paternal genotypes from within one seed origin.

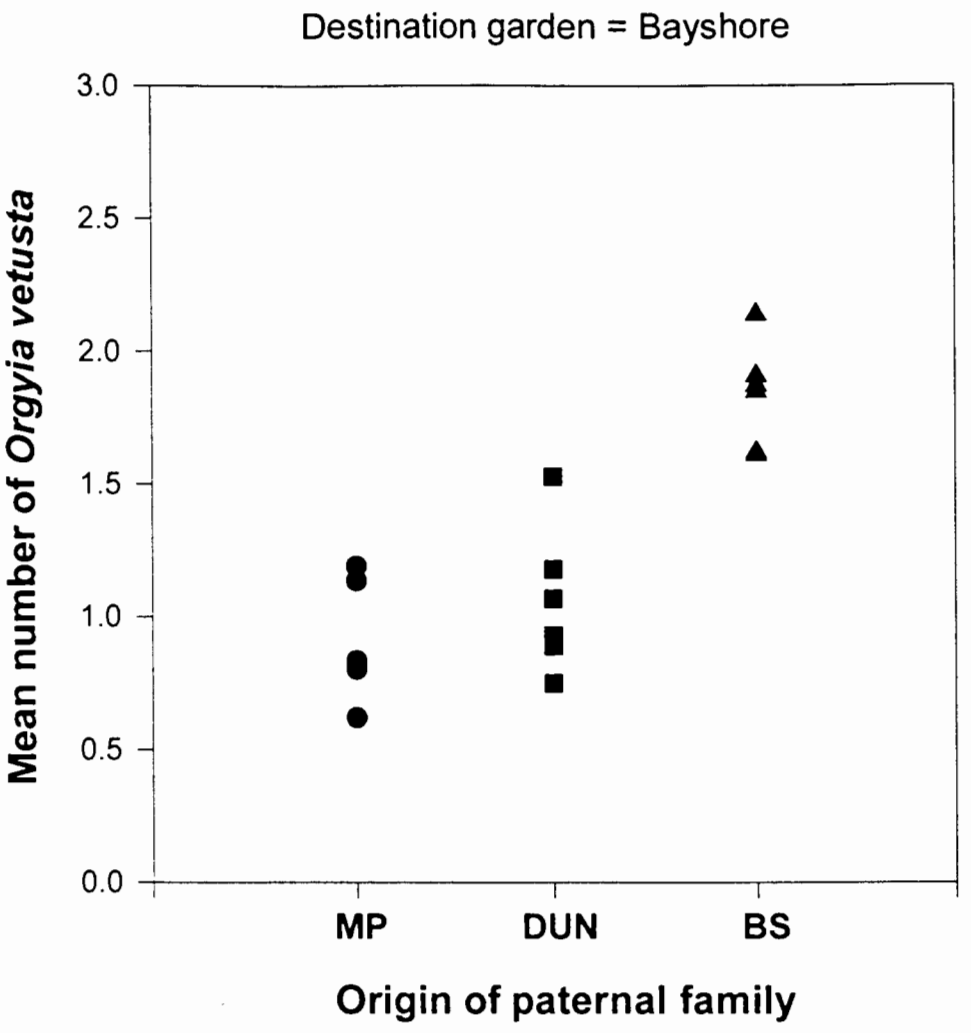

FIG. 3.—Mean number of *Orgyia vetusta* on maternal half-sib families of *Lupinus arboreus* plants in the Bayshore garden

The effect of natal seed origin, but the lack of a consistent family effect, implies that insects respond more strongly to general features of plants from one population. Characteristics of plants originating from the same population are determined in part by plant genotype. Kittelson and Maron (2001) found that lupine derived from the same seed origins used in this study are locally adapted and that genetic structure is evident among the three sites tested; thus, plants from the same population share a common evolutionary history probably because of site-specific selection. Differential insect abundance among lupine populations may be influenced by plant traits that evolved to minimize or mitigate herbivore-induced fitness reductions on roots, stems, flowers, fruits and seeds (Davidson and Barbour, 1977; Strong *et al.*, 1995; Maron and Simms, 1997; Maron, 1998; 2001; Strong *et al.*, 1999; Preisser, 2003). If I define resistance as a function of lower susceptibility to insects, then plants originating from BS appear to be least resistant; insect density was highest on BS families, regardless of destination site. Additionally, I found the highest insect loads in the BS garden. Plants from BS have unique phenotypes that express high growth rates and early seed production, both in their home garden and at other destination gardens (Kittelson and Maron, 2001); this suggests that BS plants may experience a trade-off between rapid growth, early seed set (Kittelson and Maron, 2001) and insect resistance.

Plants from DUN typically supported the smallest numbers of insects, suggesting genetic differences in susceptibility or resistance. Insects found DUN plants least suitable, as noted by Whipple (1998), who reported very low survival of *Hepialus californicus* caterpillars on DUN plants relative to grassland plants. Although neither experiment can explain why DUN lupine support smaller herbivore densities, DUN lupine are a locally adapted population (Kittelson and Maron, 2001), and one outcome of this adaptation may be increased resistance. Plants from DUN families invest more in leaf alkaloids relative to plants from other origins and, while this does not affect the apical or bud herbivores, leaf galler density was significantly affected by alkaloid concentration (Adler and Kittelson, 2004), suggesting complex interactions between herbivores and plant defenses.

In this study, I found that differences in insect densities on lupine are caused by environmental factors and partly by genetic factors present in populations of similar genotypes. Insects seemed to differentially recognize and feed on lupine that originated from the three different natal populations. Also, insect densities varied distinctly among the three environments, thus selection regimes likely differed across a small spatial scale and may contribute to the local adaptation demonstrated in a related study (Kittelson and Maron, 2002). These results indicate that interactions between insect density and plant phenotypic traits are influenced by environmental and genetic factors.

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