Narrow Hybrid Zone Between Two Subspecies of Big Sagebrush (*Artemisia tridentata*: Asteraceae): XI. Plant-Insect Interactions in Reciprocal Transplant Gardens

John H. Graham
E. Durant McArthur
D. Carl Freeman

Abstract—Basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*) hybridize in a narrow zone near Salt Creek, Utah. Reciprocal transplant experiments in this hybrid zone demonstrate that hybrids are more fit than either parental subspecies, but only in the hybrid zone. Do hybrids experience greater, or lesser, use by herbivorous insects, especially in the hybrid zone? And do certain species of herbivorous insects prefer one or the other parental subspecies of big sagebrush? We studied plant-insect interactions in three reciprocal transplant gardens that span the hybrid zone at Salt Creek. Gardens were in the basin and mountain big sagebrush zones and also in the hybrid zone. Transplanted seedlings came from two parental and three hybrid source populations. Densities of herbivorous insects varied among the gardens and source populations, but the interaction between garden and source population was statistically insignificant. Most of the variation in herbivore density was among gardens, rather than among source populations. Only grasshoppers and lepidopteran leaf miners showed significant preferences among the source populations; grasshoppers preferred mountain big sagebrush and leaf miners preferred near-basin hybrids. Coccids, *Clastoptera*, *Trirhabda*, coleophorid larvae, and lepidopteran leaf miners showed significant differences in density among the gardens. Finally, the hybrids were not a sink for herbivorous insects, nor did they have lower herbivore loads.

Introduction

Hybrid zones involving plants are natural laboratories for studying the mutual adaptations of herbivorous insects and their hosts (Strauss 1994; Fritz 1999). Thomas Whitham (1989), working on *Pemiphagus* aphid galls in a *Populus* hybrid zone, suggested that hybrids may often support much greater herbivore loads than parental taxa, and by attracting herbivorous insects may hinder adaptation to the parental taxa. He called this phenomenon the hybrid sink effect. But more recent work on a variety of plant hybrid zones has shown that the responses of insects to hybrids and parental taxa is not so simple, nor so general. Herbivorous insects may indeed prefer hybrids when coadaptation for suites of defensive chemicals has been disrupted in the hybrids, or when hybrids are stressed (Whitham 1989; Floate and others 1993; Morrow and others 1994; Whitham and others 1994; Christensen and others 1995; Kalischuk and others 1997). But insects may often show no preferences (Hanhimäki and others 1994; Graham and others 1995), or may prefer one or both parental taxa (Boecklen and Spellenberg 1990). In a single hybrid zone, Fritz and others (1994) found that some herbivores preferred hybrids, some preferred parentals, and some had no preferences.

To critically evaluate plant-herbivore interactions, reciprocal transplant experiments involving plant hybrid zones are needed (Fritz 1999). Indeed, one cannot state with certainty that a particular species of insect prefers to feed on a particular plant genotype unless both genotype and environment are controlled in a natural setting. In this paper, we show that insect use of big sagebrush hybrids and parental taxa in a reciprocal transplant experiment depends upon both genetic differences among the big sagebrush taxa and environmental differences across the hybrid zone. The environmental effects, however, are much stronger than the genetic effects.

Methods

Big Sagebrush Hybrid Zone

Big sagebrush (*Artemisia tridentata*) is the most widely distributed shrub in North America. Its environmental tolerance is extreme—from arid flats to subalpine meadows. As is true of many widely distributed species, clinal and subspecific variation is common. And different subspecies of big sagebrush hybridize, often in extremely narrow hybrid zones. For example, low elevational populations of basin big sagebrush (*A. tridentata* ssp. *tridentata*) hybridize with high elevational populations of mountain big sagebrush (*A. t.* ssp. *vaseyana*) wherever their distributions overlap. Introgression

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John H. Graham is Professor of Biology, Department of Biology, Berry College, Mount Berry, GA 30149-0446. E. Durant McArthur is Project Leader, Rocky Mountain Research Station, Provo, UT 84606. D. Carl Freeman is Professor of Biology, Department of Biological Sciences, Wayne State University, Detroit, MI 48202.

is bidirectional (McArthur and others 1988), and the hybrids consist of advanced generations and backcrosses.

Durant McArthur began studying sagebrush hybrids almost 25 years ago (McArthur and others 1979), and we (including Freeman's and McArthur's students and colleagues) have studied the hybrid zone between basin and mountain big sagebrush at Salt Creek, Utah, since 1989 (Freeman and others 1991). The parental taxa at Salt Creek differ in height, stem and leaf shape, and inflorescence structure (Freeman and others 1991), terpene and coumarin composition (Welch and McArthur 1981; McArthur and others 1988; Freeman and others 1991; Byrd and others 1999), and DNA markers (McArthur and others 1998b). We have also studied herbivory and reproduction (Graham and others 1995), developmental instability (Freeman and others 1995; Tracy and others, in preparation), and soil properties (Wang 1996; Wang and others 1998). In 1993, we began a reciprocal transplant experiment in the Salt Creek hybrid zone. This experiment was designed to critically test the predictions of three hybrid zone models: the dynamic equilibrium model, the mosaic hybrid zone model, and the bounded hybrid superiority model.

The big sagebrush hybrid zone at Salt Creek is best explained by the bounded hybrid superiority model (Wang and others 1997). This model suggests that hybrids have the highest reproductive fitness, but only in the hybrid zone (Moore 1977). The competing dynamic equilibrium model maintains that hybrid zones are stabilized by selection against hybrids, and by gene flow across the zone (Barton and Hewitt 1985); the hybrid zone is independent of the environment. And the mosaic hybrid zone model maintains that exogenous selection acts against hybrids, but that parental taxa are adapted to different environments (Harrison and Rand 1989; Arnold 1997).

Studies in the transplant gardens at Salt Creek have included reproductive fitness (Wang and others 1997; Freeman and others 1999), respiration and water potential (McArthur and others 1998a), nutrient uptake (Wang 1996; Wang and others 1999), and growth (Freeman and others 1999). These studies are summarized in Graham and others (1999). Current research involves taxon-specific soil mycorrhizal associations (Miglia and others, unpublished data) and developmental stability (Graham and others, unpublished data). Graham and others (1995) studied the distribution and use of big sagebrush by gall-formers, grasshoppers, aphids, and deer in the hybrid zone, but this research did not involve the transplant gardens. Messina and others (1996) looked at insects on hybrid and parental sagebrush grown in a single common garden, but the garden was not actually in a hybrid zone.

Study Site

The reciprocal transplant gardens span the big sagebrush hybrid zone at Salt Creek, near Nephi, Utah (Uinta National Forest, Juab Co., Fountain Green North Quadrangle). Basin big sagebrush occur along Salt Creek and its tributaries, to an elevation of about 1,790 m. Mountain big sagebrush occur from about 1,850 m to timberline on nearby Mt. Nebo. The hybrids occur from 1,790 to 1,830 m elevation, in a narrow band between the basin and mountain populations (Freeman and others 1991).

We studied five stands of big sagebrush at Salt Creek: the two parental subspecies and three classes of hybrids. We refer to *A. t.* ssp. *tridentata* as **basin**, *A. t.* ssp. *vaseyana* as **mountain**, the middle hybrid as **hybrid**, the hybrid between basin and middle hybrid as **near basin**, and the hybrid between mountain and middle hybrid as **near mountain**.

Reciprocal Transplant Gardens

We germinated seeds from the five source populations (basin, near basin, hybrid, near mountain, and mountain), grew the seedlings for one year in a greenhouse, and planted twelve seedlings from each source in each of three gardens (basin, hybrid, mountain) during May 1993. The gardens were enclosed with 2.5 m high fences, for protection from elk, deer, and cattle.

The basin garden is on a bench just above the flood plain of Salt Creek, at an elevation of 1776 m. The mountain garden is on the lower slope of Mt. Nebo, at an elevation of 1870 m. The hybrid garden is in a relatively flat meadow, at an elevation of 1800 m, and midway between the basin and mountain gardens. (See Wang and others [1997] for additional details.)

Census of Insects

We counted insects on big sagebrush in our three gardens during the week of June 21-27, 1997. Although this is a relatively brief sampling period, it occurs at a time of year when insect activity on sagebrush is at a peak. Respiration rates and water potential reach their seasonal peaks in early summer (McArthur and others 1998a), and temperatures are not yet warm enough to restrict insect activity. For grasshoppers, we counted both the insects and the physical evidence of their browsing. And because the ant *Formica dakotensis montigena* makes its nest below ground, at the base of sagebrush, we only recorded its presence or absence on a plant. Samples of all insects were preserved in 70 percent ethanol for later identification.

Plant size may influence numbers and diversity of insects. To estimate density of herbivores, we needed an estimate of relative plant volume. A measure of volume is $v = hc^2$, where h is height and c is crown diameter. This is a measure of the volume of the smallest square-ended box enclosing a plant.

Statistical Analysis

Plant size varied among gardens and taxa, so we expressed all counts as densities (i.e. number divided by v). We used MANOVA to compare insect densities of the most common insect species among gardens and source populations. We used a crossed design, with replication. Individual plants (the replicates) were nested within the garden by source population. Both garden and source were fixed variables in the MANOVA. A separate MANOVA was done for the three main guilds of insects: chewers, suckers, and gall-formers. (Data on the gall-formers is from Graham and others 2001). As an adjunct to the MANOVAs, we also performed univariate two-way ANOVAs for each variable. We used analysis of covariance (ANCOVA) to compare insect diversities among gardens and source populations.

Most of the insects on sagebrush had contagious (clumped) distributions. Southwood (1978) recommends a logarithmic transformation for highly contagious distributions. We found that a logarithmic transformation of the densities ($\log_{10}[x + 1]$) gave the best approximation to a normal distribution, and stabilized the variance.

Results

Herbivore Density and Distribution

Herbivorous insects on big sagebrush included several orthopterans, homopterans, lepidopterans, and coleopterans (table 1). Dipteran gall-formers, which were also present, are treated in a separate paper (Graham and others 2001). There were significant differences in densities of herbivores among the three gardens and five source populations (table 2). The effect of garden, however, was more highly significant than that of source population. Five herbivores (coccids, spittlebug larvae, *Trirhabda pilosa*, coleophorid larvae, and leaf miners) differed significantly among gardens, while only two species (grasshoppers and leafminers) differed significantly among source populations. Gardens by source population interactions were insignificant.

Herbivorous insects fall into three feeding guilds: leaf chewers and miners, phloem and xylem suckers, and gall-formers. Leaf chewers include the grasshoppers, chrysomelid beetles, and lepidopteran larvae. Grasshoppers (*Melanoplus* sp. and other species) were in low densities in all three gardens, but preferred mountain big sagebrush (fig. 1).

Both larval and adult chrysomelids fed on big sagebrush. *Trirhabda pilosa* has a metallic-green larva that can inflict significant damage on sagebrush. The larvae were only on a few plants in the hybrid garden. In contrast, the adults were only in the basin garden (fig. 2). The larva and adult *Exema conspersa* feed on leaves. Their densities did not vary among gardens or source populations (table 2 and fig. 2). Other coleoptera, such as weevils (*Sternechus* sp.) and scarabid beetles, (*Dichelonyx* sp.) were rare.

Larval lepidoptera included a pterophorid moth, a case-bearing coleophorid moth, and an unidentified leaf miner. All three species feed on leaves. While the pterophorids were uncommon, the more abundant coleophorids differed significantly among gardens (table 2), and were most abundant in the basin garden (fig. 3). Leaf miner densities varied among gardens and source populations (table 2). They were more abundant in the mountain garden, and preferred near-basin plants (fig. 3).

Phloem and xylem suckers include the aphids, coccids, spittlebugs, leafhoppers, cicadas, and true bugs. Two species of aphids were *Obtusicauda coweni* and *O. filifoliae*. Neither showed significant differences in density among gardens or source populations (table 2 and fig. 4). Coccids (scale insects) showed significant differences among gardens (table 2). They were most common in the basin garden, absent from the mountain garden, and of intermediate abundance in the hybrid garden (fig. 5). Spittlebugs (*Clastoptera* sp.) showed significant variation among gardens (table 2). They were also most abundant in the basin garden (fig. 5). Leafhoppers, cicadas, and true bugs (*Lygus* sp.) were rare.

Table 1—Insects found on big sagebrush in the reciprocal transplant gardens.

Scientific name	Family: Order	Description
Herbivorous Insects		
Melanoplus sp.	Acrididae: Orthoptera	Browsing on stem
Unknown grasshoppers	Acrididae: Orthoptera	Browsing on stem
Obtusicauda coweni	Aphididae: Homoptera	Black phloem-feeding aphid
Obtusicauda filifoliae	Aphididae: Homoptera	Green phloem-feeding aphid
Scale Insect	Coccidae: Homoptera	Phloem feeder
Clastoptera sp.	Cercopidae: Homoptera	Phloem-feeding nymph
Leafhopper	Cicadellidae: Homoptera	Phloem feeder
Cicada	Cicadidae: Homoptera	Phloem feeder
Lygus sp.	Miridae: Hemiptera	Phloem feeding larva and adult
Sternechus sp.	Curculionidae: Coleoptera	Leaf chewing adult
Trirhabda pilosa	Chrysomelidae: Coleoptera	Leaf chewing larva and adult
Exema conspersa	Chrysomelidae: Coleoptera	Case-bearing larva and leaf chewing adult
Octinodes sp.	Elateridae: Coleoptera	Non-feeding adult
Dichelonyx sp.	Scarabaeidae: Coleoptera	Leaf chewer
Lyctus sp.	Lyctidae: Coleptera	Wood borer
Moth larva	Pterophoridae: Lepidoptera	Leaf chewing caterpillar
Casebearing moth	Coleophoridae: Lepidoptera	Leaf chewing caterpillar
Unidentified moth larva	Lepidoptera	Leaf miner
Non-herbivorous Insects, and other Arthropods		
Hippodamia apicaulis	Coccinellidae: Coleoptera	Ladybird beetle
Formica dakotensis	Formicidae: Hymenoptera	Nest at base of plant
Monomorium minimum	Formicidae: Hymenoptera	Tending coccids
Wasp	Hymenoptera	
Spider	Aranae	

Table 2—Multivariate and univariate ANOVAs for the effects of garden, source, and garden by source interaction on density of herbivorous insects.

MANOVA

Source	Df	Wilks' λ	*F*	*P*
Garden	18, 240	0.28962	11.44244	<0.001
Source	36, 451	0.66124	1.46339	0.044
Garden x Source	72, 737	0.49543	1.25367	0.083

Univariate ANOVAs (*F* statistics)

	Effect (degrees of freedom in parentheses)		
Insect	Garden (2, 128)	Source (4, 128)	Garden x Source (8, 128)
Acrididae	2.564	2.495 *	1.275
Obtusicauda coweni	0.888	2.091	1.240
Obtusicauda filifoliae	1.718	0.638	0.733
Coccidae	10.239 ***	1.283	1.627
Clastoptera sp.	7.480 **	0.660	1.908
Exema conspersa	1.914	1.238	0.488
Trirhabda pilosa	6.266 **	2.327	1.561
Coleophoridae, larva	4.488 *	0.276	0.873
Leaf Miners	95.587 ***	3.393 *	1.976

* $P<0.05$.
** $P<0.01$.
*** $P<0.001$.

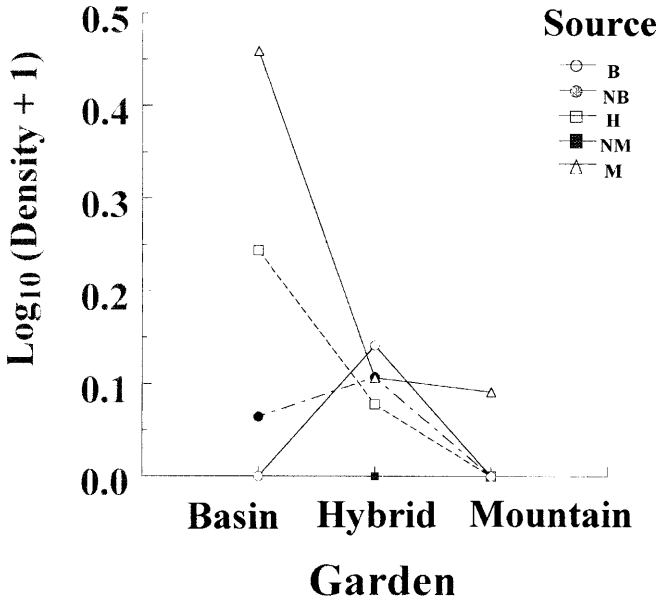

Figure 1—Interaction of garden and source population on density of hoppers and hopper browse. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

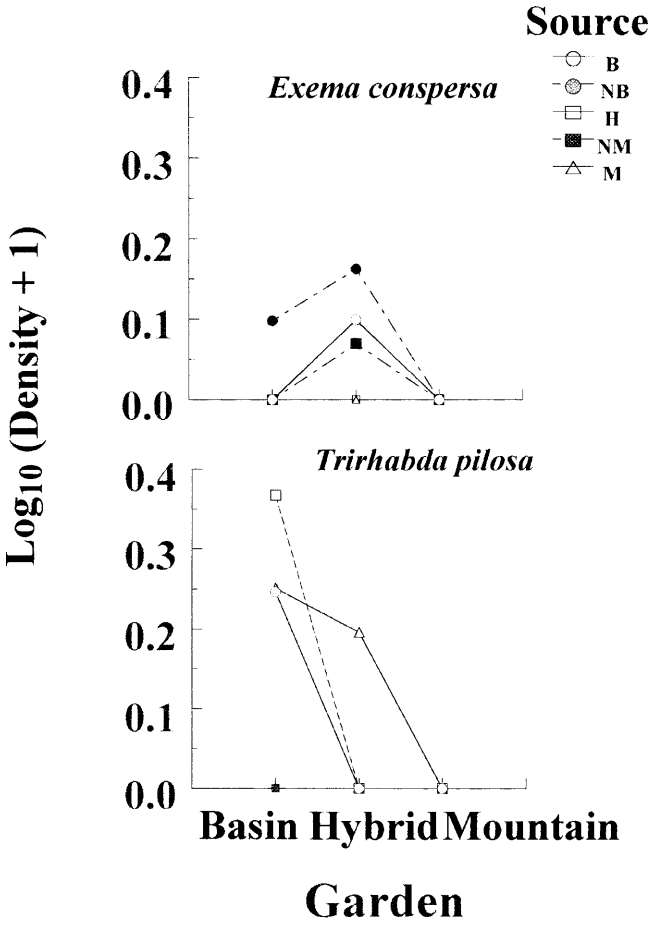

Figure 2—Interaction of garden and source population on density of coleopteran adults and larvae of *Exema conspersa* and *Trirhabda pilosa*. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

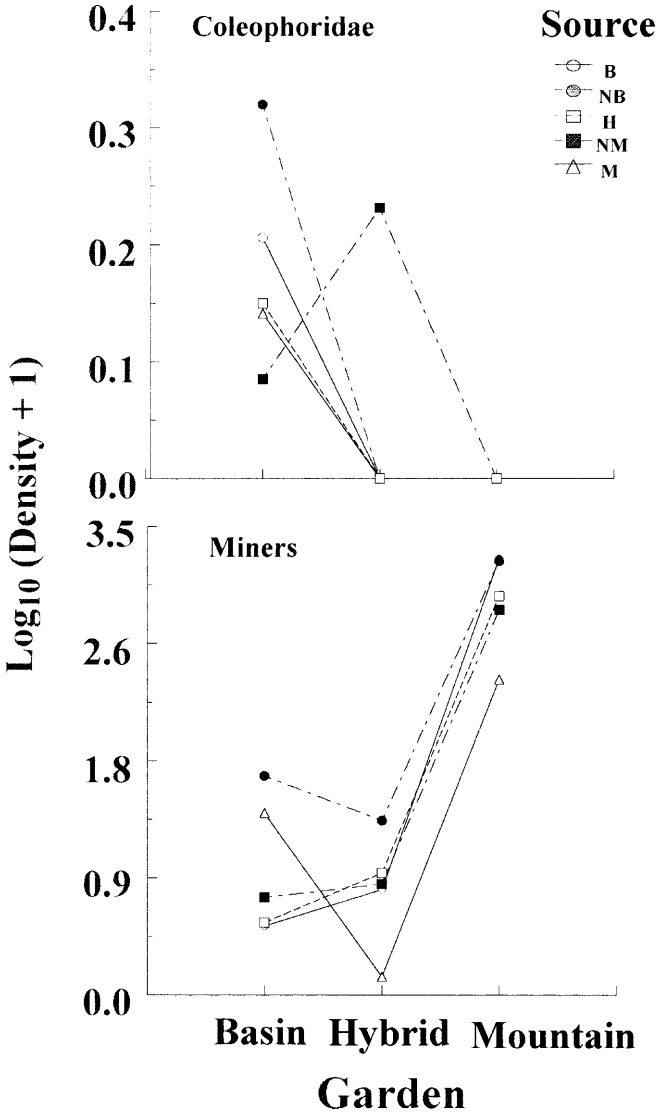

Figure 3—Interaction of garden and source population on density of coleophorid larvae and lepidopteran leaf miners. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

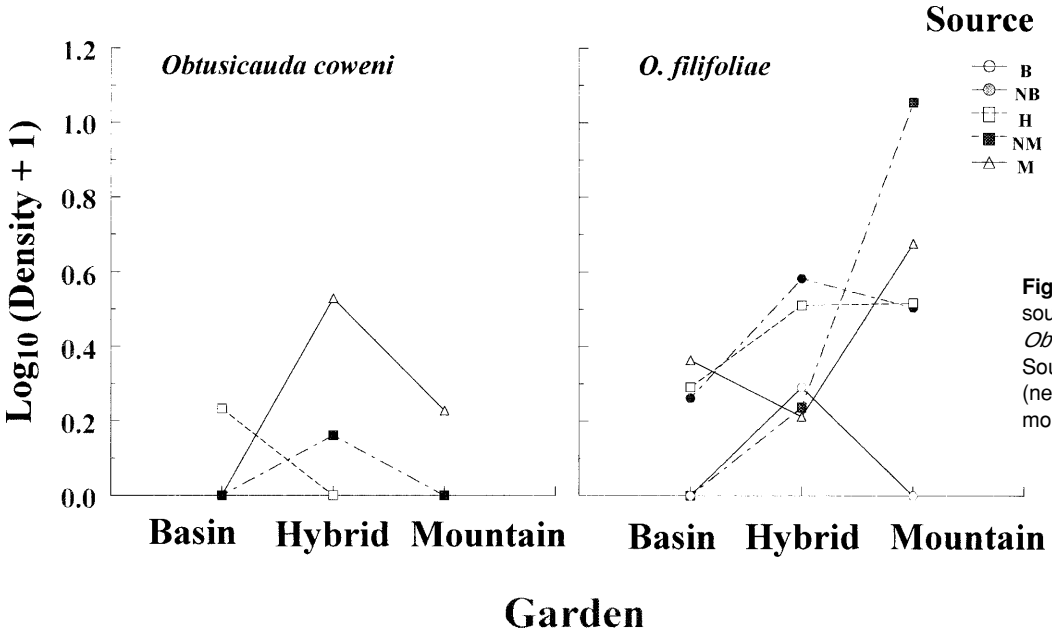

Figure 4—Interaction of garden and source population on density of aphids *Obtusicauda coweni* and *O. filifoliae*. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

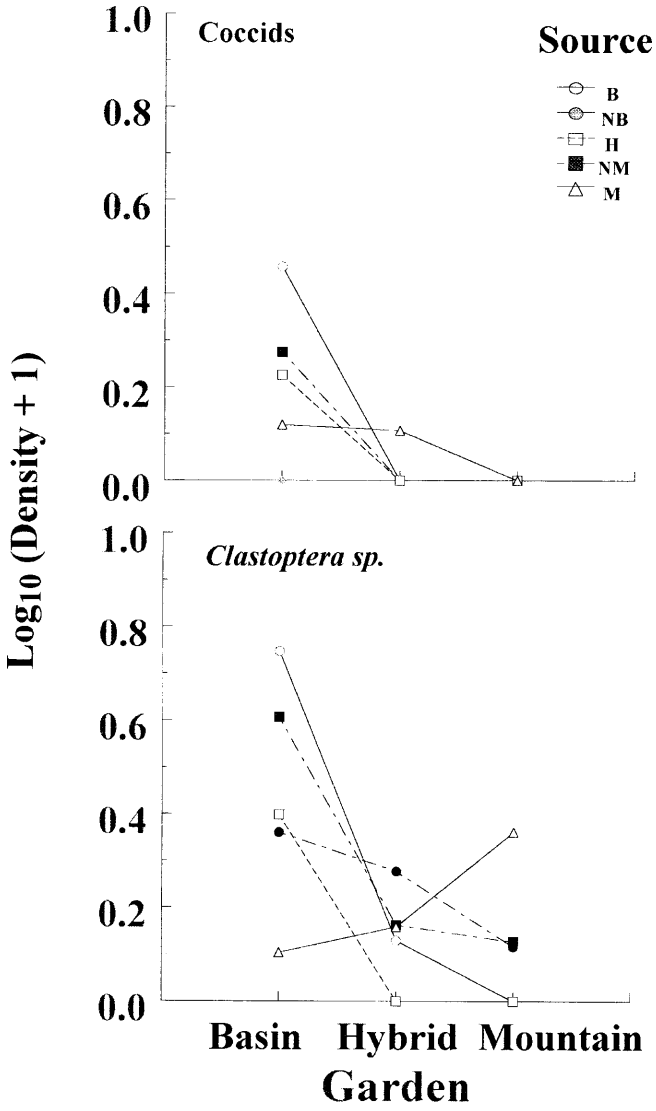

Figure 5—Interaction of garden and source population on density of coccids and spittlebug (*Clastoptera* sp.) larvae. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

The three guilds (leaf chewers and miners, phloem and xylem suckers, and gall-makers) showed significant differences in density among gardens and source populations (table 3). (Data on gall-formers is from Graham and others [2001]). There was also a significant garden by source population interaction (fig. 6). Gall-makers were the most abundant of the three guilds; phloem suckers were the least abundant. Densities of galls and leaf chewers and miners were highest in the mountain garden, but varied with source population (fig. 6). Phloem suckers did not differ significantly among gardens or source populations (table 3).

Herbivore Diversity

Do garden and source population have an effect on species diversity of herbivorous insects? Because the size of a plant may also influence the species diversity of insects, we used analysis of covariance to eliminate the effect of plant size. The effect of plant size ($\log_{10}$ [v + 1]) on species diversity ($\log_{10}$ [S + 1]), where S is the number of species, was both linear and homogeneous with respect to garden, source, and garden by source, for herbivores.

Diversity of herbivorous insects depends upon both shrub size and garden (table 4). The number of herbivorous species increased with increasing plant volume (b = 1.4695, t = 2.661, P = 0.009). And the hybrid garden had fewer species of herbivorous insects than either the basin or mountain gardens (fig. 7).

Table 3—Multivariate and univariate ANOVAs for the effects of garden, source, and garden by source interaction on density of three guilds. Data on galls is from Graham and others (2001).

MANOVA

Source	Df	Wilks' λ	*F*	*P*
Garden	6, 252	0.17658	57.95019	<0.001
Source	12, 334	0.71593	3.74334	<0.001
Garden x Source	24, 366	0.71834	1.84275	0.010

Univariate ANOVAs (*F* statistics)

	Effect (degrees of freedom in parentheses)		
Guild	Garden (2, 128)	Source (4, 128)	Garden x source (8, 128)
Chewers and miners	90.257 ***	4.268 **	2.488 *
Suckers	0.179	0.759	1.100
Gall-formers	128.935 ***	6.340 ***	2.202 *

* P<0.05.
** P<0.01.
*** P<0.001.

Incidental Nonherbivores

The nonherbivorous arthropods included two species of ants (*Formica dakotensis montigena* and *Monomorium minimum*). *Formica d. montigena* nested under leaf thatch below the canopy, and around the trunk, of individual plants. These large red and black ants vigorously defended their nests, and plants. *Formica dakotensis* was more common in the mountain garden, but showed no obvious preference for sagebrush from any of the five source populations. Presence of a *Formica* nest at the base of a plant had no effect on the diversity of herbivores and galls (MANCOVA, $F_{2, 139}$ = 0.088, P = 0.916) or on the density of leaf chewing insects and sucking insects (MANCOVA, $F_{2, 137}$ = 0.802, P = 0.451). The smaller black ant (*Monomorium minimum*), restricted to the basin garden, was usually associated with, and tending, coccids. Its density was correlated with coccid density (r = 0.5339, df = 142, P <0.001), but not with aphid density (r = 0.0338, df = 142, P >0.50).

Several predatory arthropods were present on the sagebrush. The ladybird beetle *Hippodamia apicaulis* was fairly common, as were several species of unidentified spiders. The click beetle (*Octinodes* sp.) and lyctid wood borer (*Lyctus* sp.) were rare. Occasional wasps were seen, but not collected.

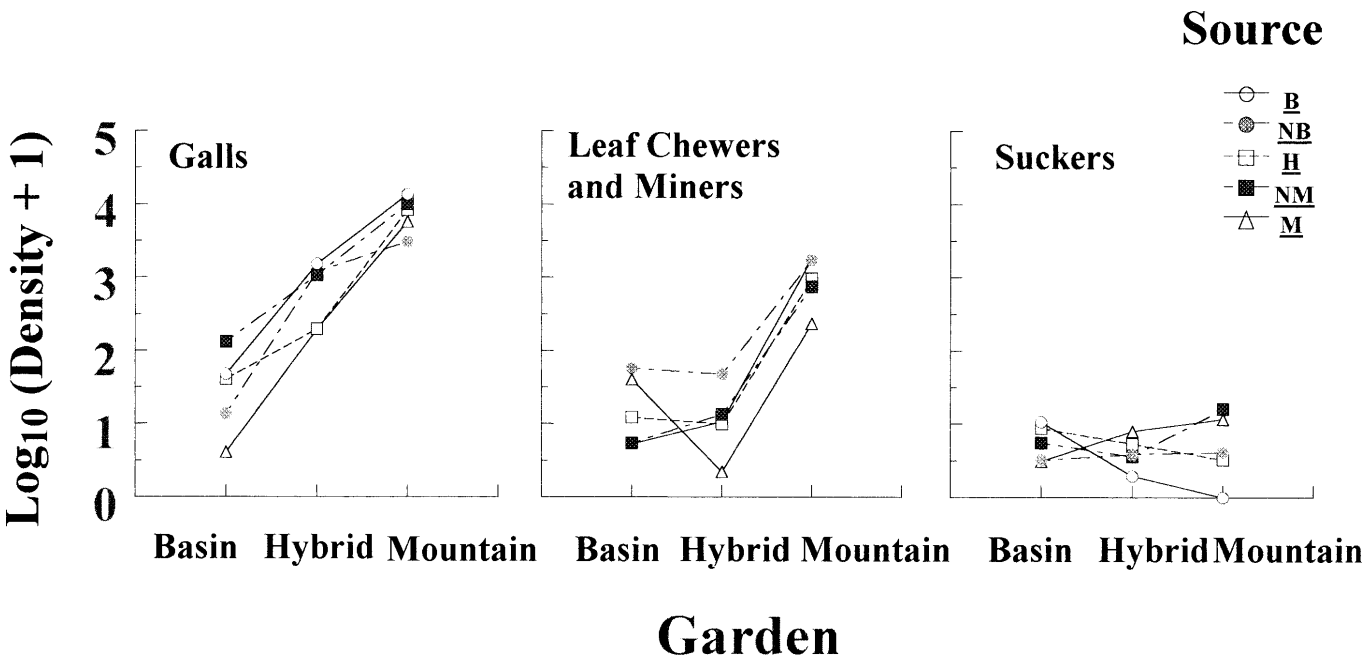

Figure 6—Summary of interactions of garden and source population on densities of leaf chewers and miners, and phloem suckers. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

Table 4—Analysis of covariance for the effects of garden and source population on diversity of herbivorous insects ($\log_{10}[S+1]$). Plant volume ($\log_{10}[V+1]$) is the covariate.

Source	Df	MS	*F*	*P*
Garden	2	0.23	8.09	<0.001
Source	4	0.01	0.49	0.743
Garden x Source	8	0.02	0.87	0.545
Size	1	0.20	7.08	0.009

Discussion

Densities of herbivorous insects on hybrid and parental big sagebrush vary with both genotype and environment. Messina and others (1996) found that herbivore use of hybrid and parental big sagebrush in a common garden in northern Utah depended upon plant genotype. Our experiment extends their results by examining hybrids and parentals in reciprocal transplant gardens that span an actual hybrid zone. Of the two main effects, environment (garden) had a greater effect on herbivore density than did genotype (source population). We found the same pattern for gall-formers (Graham and others 2001). Nevertheless, gall-formers showed significant genotype-environment interactions, while none of the individual species of chewers and suckers did.

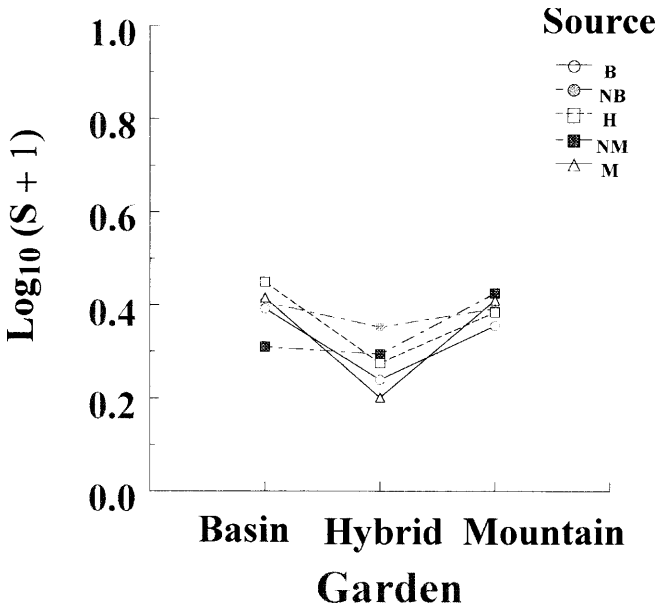

Figure 7—Interaction of garden and source population on diversity of herbivorous insects, after removing the effect of plant volume on diversity. Source populations are B (basin), NB (near basin), H (hybrid), NM (near mountain), and M (mountain).

Among the herbivorous insects, only the grasshoppers and leaf miners showed any evidence of host specificity. Grasshoppers were absent from near-mountain plants, but this may result from sampling bias, since their densities were low. Leaf miners clearly preferred near-basin plants, but they were present on all five populations.

Aphids of the genus *Obtusicauda* are *Artemisia* specialists (Robinson and Halbert 1989). Graham and others (1995) found more aphids on middle and near-mountain hybrids in 1989. Nevertheless, in 1997 we found no evidence of specialization on hybrids or parental subspecies by either *O. filifoliae* or *O. coweni*. *Obtusicauda coweni* and *O. filifoliae* were equally common in all three gardens, and showed no preferences among the five source populations. Greater densities of aphids on hybrids in 1989 may have been related to rainfall patterns in that year, and also to the time of year the aphids were censused (August). In July, water potential of sagebrush is still high in all three gardens, but by September, plants in the mountain garden are experiencing greater water stress than those in either the hybrid or basin gardens (McArthur and others 1998a). Low water potential can reduce sap intake by aphids, resulting in lower reproductive potential or movement to new plants (Kennedy and Stroyan 1959). Thus, in some years spatial and temporal variation in aphid density and distribution may result from environmental and temporal variation in water availability (Moran and Whitham 1988).

Herbivorous insects may severely affect the fitness of individual plants. The chrysomelid beetle *Trirhabda pilosa* can defoliate and kill entire populations of big sagebrush, especially at higher elevations (Pringle 1960). Both larvae and adults are leaf chewers. We found no evidence of such high population densities in our gardens. In the 10 years we have studied the hybrid zone at Salt Creek, we have not seen defoliation by *Trirhabda*. Only a small number of plants were infested with either larvae (in the hybrid garden) or adults (in the basin garden). The distribution of larvae and adults in the hybrid and basin gardens is probably related to timing of emergence. After reaching a length of about 10 mm, larvae drop off the host plant, pupate in the soil, and emerge as adults 1 to 2 weeks later (Pringle 1960). In August 1998, we observed many adults in the mountain garden, so we were probably sampling too early in 1997 to find larvae or adults in the mountain garden.

Incidental arthropods may have a significant influence on plant-herbivore interactions. Ants often interact with aphids, and in the process reduce herbivory by leaf-chewing insects (Pringle 1960; Floate and Whitham 1994). They also prey on ovipositing *Rhopalomyia* (Jones and others 1983). We did not, however, find a significant association of *Formica dakotensis* or *Monomorium minimum* with aphids, nor a negative association with either galls or leaf chewing insects. This is true despite the fact that *Formica* vigorously defended individual plants. *Formica dakotensis* is a temporary social parasite on the *F. fuscus* group (Wheeler and others 1994). *Formica obscuripes*, another member of the *rufa* group, also nests under sagebrush, and is known to kill and remove the plant from its nest (Cole 1932, as cited by Creighton 1950). According to Robinson and Halbert (1989), *Obtusicauda* aphids are not tended by ants. *Monomorium minimum* was found tending scales, rather than aphids.

Conclusion

Only grasshoppers and leafminers appear to distinguish among hybrid and parental genotypes. Coccids, *Clastoptera*, *Trirhabda pilosa*, coleophorid larvae, and lepidopteran leaf miners, on the other hand, all show more significant variation among environments. Most importantly, hybrids in the big sagebrush hybrid zone are not more heavily grazed than the parental taxa; the hybrid zone is not a sink for herbivores. Nor do they experience less grazing than the parental taxa in the hybrid zone. Insects vary along the elevational gradient, and a few also seem to target particular taxa.

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