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Characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*, Asteraceae): VII. Community and demographic analyses

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ABSTRACT

We examined the floristic and vegetative composition of the communities inhabited by basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*) and their hybrids in Clear Creek Canyon near Richfield, Utah. We also examined the demographic structure of the sagebrush populations in their native habitats. The species composition, proportions of annual plants, perennial forbs and grasses, shrubs, rock, litter, bare ground and total vegetative cover differ among the parental sites and hybrid zone. Canonical correspondence analysis and ordination showed that the two big sagebrush subspecies and their hybrids are each associated with different groups of species, and occupy edaphically distinct habitats. Thus, the hybrid zone occurs at an ecotone. Moreover, the hybrid zone is not in a more disturbed habitat than the parental zones. Indeed, annuals comprise a significantly smaller fraction of the total vegetation in the hybrid zone than in either parental zone. Similarly, introduced species represent a significantly greater percentage of the plant cover in the parental areas than in the hybrid zone. We did not observe a population density trough as predicted by the dynamic equilibrium model. Our findings are consistent with the predictions of the bounded hybrid superiority model, which postulates that hybrids occupy unique habitats.

Keywords: big sagebrush, canonical correspondence analysis, community composition, demographic structure, ecotone, hybrid zone, ordination.

INTRODUCTION

Hybrid zones are important because the genetic variation within the zones (the transition region between the parental taxa) is spatially structured, forming clines or mosaic patterns

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that potentially reflect underlying environmental heterogeneity. The basic models proposed to account for the persistence of stable hybrid zones assume that dispersal is balanced by selection, thereby stabilizing the width of the hybrid zone (Moore, 1977; Barton and Hewitt, 1985). However, the models differ in their assumptions about that selection. The ecologically neutral dynamic equilibrium model assumes that hybridization disrupts co-adapted gene complexes, thereby adversely impacting developmental or physiological processes. The resulting hybrid progeny, then, should be relatively unfit (Barton and Hewitt, 1985, 1989). Because this reduction in fitness is due to internal factors, selection against hybrids is presumed to be independent of the environment (for references and a more complete discussion, see Barton and Hewitt, 1985; Moore and Price, 1993). Accordingly, the point of equilibrium (the hybrid zone) can move until it encounters areas of low population density where it becomes trapped (Key, 1968; Bazykin, 1969; Barton and Hewitt, 1985).

In contrast, the bounded hybrid superiority model assumes that selection results from genotype by environment interactions, and that within the hybrid zones, hybrids are equally or more fit than either parental taxon (Endler, 1977; Moore, 1977; Moore and Price, 1993). Selection, in this case, leads to ecological adaptation with the parental taxa and their hybrids each adapted to their own environment. Accordingly, both the position and stability of hybrid zones are due to ecological selection. Inherent in the bounded hybrid superiority model is the assumption that hybrid zones should occur in areas with profound environmental gradients, and that the hybrids themselves occupy a unique environment (i.e. an ecotone). Critical tests of these models should examine the environment in the hybrid zone and parental areas abutting the hybrid zone.

Remarkably few investigators have examined the nature of the environment in which stable hybrid zones occur (however, see White and Chinnick, 1957; Howard, 1986; Kohlmann *et al.*, 1988; Nichols and Hewitt, 1988; Cruzan and Arnold, 1993; Moore and Price, 1993; Emms and Arnold, 1997). Some authors (e.g. Howard, 1986; Moore and Price, 1993) have suggested that hybrid zones are associated with ecotones, but others (White and Chinnick, 1957; Nichols and Hewitt, 1988) have reported no such association. Analysis of the environment of stable hybrid zones is important, because it may distinguish between competing models seeking to explain the maintenance of stable hybrid zones and illuminate the role of ecological adaptation in speciation.

Botanists routinely find that plant species are closely associated with particular environmental factors, and often have poor growth and low rates of reproduction when transplanted into alien environments (Clausen *et al.*, 1940; Briggs and Walters, 1984). Most of these studies conclude that ecological adaptation determines the ranges of the parental taxa, but there are exceptions (Levin and Schmidt, 1985; Potts and Reid, 1985). Findings of ecological adaptation by the parental taxa to their native habitats in allopatric areas do not distinguish between the competing hybrid zone models, because the dynamic equilibrium model does not address ecological adaptation in areas of allopatry. Few studies have examined the fitness of the parental taxa within the hybrid zone, and the fitness of the hybrids in the parental zones. Levin and Schmidt (1985) and Schmidt and Levin (1985) examined the fitness of individuals in the *Phlox drummondi* hybrid zone. They did not find a consistent alien disadvantage, as predicted by the bounded hybrid superiority model, or hybrid unfitness, as predicted by the dynamic equilibrium model. Indeed, the phlox hybrid zone was so broad,

with such low gene flow, that little or no selection is required to stabilize the zone (the selection coefficient, S, would need to be on the order of 10^{-5} or 10^{-6} and thus effectively neutral). Emms and Arnold (1997) showed that hybrids of *Iris fulva* and *I. hexagona* are able to reproduce clonally at least as well as the parental taxa in all transplant gardens.

We found clear evidence of significant genotype by environment interactions for most life-history parameters in the big sagebrush hybrid zone (Wang *et al.*, 1997). More importantly, hybrids were overwhelmingly *more* fit than either parental taxon within the hybrid zone. Strong exogenous selection stabilized the big sagebrush hybrid zone ($S \propto 10^{-1}$). These results are in agreement with the bounded hybrid superiority model. We also examined edaphic properties of the habitats occupied by the parental taxa and their hybrids. We found that the parental zones differed from one another in soil depth, pH and elemental composition. Soils from the hybrid zone differed significantly from those of either parental region, and were spatially more variable than those of the parental zones (Wang *et al.*, 1997, 1998).

Here, we further test the prediction that the big sagebrush hybrid zone should occupy an ecotone by examining the composition of plant communities in the parental and hybrid zones. Concordance among species distributions, coupled with the already observed discontinuity in the soils, would indicate the existence of an ecotone, while the lack of such concordance would indicate the absence of an ecotone. We also examined the population density across the big sagebrush hybrid zone to determine if it occurs in a population density trough as postulated by the dynamic equilibrium model. This is important because the predictions of the two models are not mutually exclusive.

BACKGROUND INFORMATION

Artemisia tridentata (big sagebrush) is a common shrub in western North America. The species consists of five subspecies: *A. t.* ssp. *tridentata* (basin big sagebrush), *A. t.* ssp. *vaseyana* (mountain big sagebrush), *A. t.* ssp. *wyomingensis*, *A. t.* ssp. *spiciformis* and *A. t.* ssp. *xericensis* (Rosentreter and Kelsey, 1991; McArthur, 1994). The species is long-lived (several decades) and wind-pollinated, with limited seed dispersal (most seeds fall within 2 m of the parent; Wagstaff and Welch, 1990). The two subspecies of interest here, basin big sagebrush and mountain big sagebrush, are parapatrically distributed in the region. At our study sites in Utah, basin big sagebrush grows below 1770 m in elevation, while mountain big sagebrush grows above 1870 m in elevation. The two subspecies hybridize and form a stable and narrow hybrid zone in a belt between these two elevations (McArthur *et al.*, 1988; Freeman *et al.*, 1991; Wang *et al.*, 1998).

We have characterized the two subspecies and their hybrids using several phenotypic traits and genetic markers. Big sagebrush produces three coumarins not found in mountain big sagebrush. Mountain big sagebrush produces one coumarin not found in basin big sagebrush (Freeman *et al.*, 1991). Basin and mountain big sagebrush each produce terpenes not found in the other subspecies (25 in the case of basin and 3 in the case of mountain; Byrd, 1992; Weber *et al.*, 1994). The subspecies differ in size and a number of morphological traits (Freeman *et al.*, 1991). Hybrid indices based upon either morphology or secondary compounds are highly correlated (Byrd *et al.*, 1999), indicative of hybrid zones (Barton, 1983; Barton and Hewitt, 1985). McArthur *et al.* (1998a) recently found 22 RAPD markers

and three RFLP markers that distinguish the parental taxa. Common garden studies of controlled crosses (F_1 and F_2) show that the terpenes (McArthur *et al.*, 1988; Weber *et al.*, 1994) and the RAPD markers (McArthur *et al.*, 1998a) are inherited in a Mendelian manner. The terpene markers display co-dominance, while the RAPD markers display simple dominance. Clearly, the parental taxa are genetically, biochemically and morphologically distinct. Hybrids are intermediate for most traits examined, although they do produce some terpenes not found in either parental taxon (Byrd, 1992; Weber *et al.*, 1994; Rieseberg and Ellstrand, 1993, document a number of other cases where hybrids are not intermediate).

The present distribution of big sagebrush taxa probably dates to the end of the Wisconsin glaciation, 12,000 years ago (Axelrod, 1950; McArthur *et al.*, 1981), although the parental populations have been in contact since the late Tertiary or early Quaternary (Axelrod, 1950). The hybrid zone, although usually less than 1 km wide, may range from less than 100 m to several kilometres in width and appears stable (Freeman *et al.*, 1991; Wang *et al.*, 1998).

We have studied six different hybrid zones between basin and mountain big sagebrush: Diamond Fork, Utah County, Utah (McArthur *et al.*, 1988); Salt Creek Canyon, Juab County, Utah (Freeman *et al.*, 1991, 1995; Byrd, 1992; Graham *et al.*, 1995; Wang *et al.*, 1997, 1998, in press; Byrd *et al.*, 1999; McArthur *et al.*, 1998b); Orem, Utah County, Utah (Freeman *et al.*, 1991, 1995; Graham *et al.*, 1995); Clear Creek Canyon, Sevier County, Utah (Wang, 1996; Wang *et al.*, 1998); Scipio Canyon, Millard County, Utah (D.C. Freeman and E.D. McArthur, unpublished data); and Rio Grande Drainage, Custer County, Idaho (E.D. McArthur, S. Sanderson and D.C. Freeman, unpublished data). In two of these hybrid zones (Clear Creek Canyon and Rio Grande Drainage), a third taxon of big sagebrush, Wyoming big sagebrush (*A. t.* ssp. *wyomingensis*), is also present. Basin and mountain big sagebrush are, for the most part, diploid ($x = n = 9$), but tetraploid populations and tetraploid individuals in otherwise diploid populations are known to occur (McArthur *et al.*, 1981; McArthur and Sanderson, submitted). These tetraploids are thought to be autotetraploids based upon a high frequency of quadrivalents (McArthur *et al.*, 1981) and similar RAPD markers to adjacent diploid populations (McArthur *et al.*, 1998b). Wyoming big sagebrush is uniformly tetraploid (McArthur *et al.*, 1981; McArthur and Sanderson, submitted) and could potentially breed with tetraploid basin or mountain plants. Wyoming big sagebrush was originally described as being a hybrid derivative from basin and mountain big sagebrush (Beetle and Young, 1965). Stebbins (1971) argued that unidirectional introgression from diploids to tetraploids is a natural phenomenon. Thus, it is unlikely that gene flow would go from these tetraploids to the diploid basin and mountain big sagebrush (the subjects of this study).

McArthur and Sanderson (submitted) report chromosome counts from the hybrid zones. A few tetraploid plants are usually present in predominately diploid populations. Consequently, the two sites that include Wyoming big sagebrush may have hybrid plants that are difficult to distinguish from Wyoming big sagebrush plants or vice versa. At the Clear Creek Canyon site (the site of this study), Wyoming big sagebrush plants clearly occupy the dry, steep canyon slopes, whereas basin and mountain big sagebrush form a cline, together with their apparent hybrids (and potentially some Wyoming big sagebrush plants), on an elevational gradient from the mouth of Clear Creek to the summit of Cove Fort Pass. Thus, it is possible that we may have grouped some Wyoming big sagebrush plants in with the basin × mountain big sagebrush hybrids.

MATERIALS AND METHODS

Site description and vegetation sampling

Clear Creek Canyon near Richfield, Utah (Fig. 1) was chosen for study because the hybrid zone there is relatively undisturbed, and its flora is overwhelmingly native (see Appendix). One sampling site was located in each of the parental zones and at two locations within the hybrid zone. Within each site, a modified Daubenmire index (Wang, 1996) was used to estimate the cover of each species in 20 one-metre square quadrats. We recorded the cover, by species, in the same quadrats, in both August 1992 and May 1993. The two sets of data were pooled for analysis. In addition, we estimated the cover of litter, rock and bare ground. Species were classified by life form group (tree, shrub, perennial forb, perennial graminoid and annual). We also noted whether species were native or introduced. From these data we calculated the Shannon Weaver diversity index, H' (Ludwig and Reynolds, 1988).

Floristic composition

The numbers of families, genera and species found in each of the four sites were tabulated. The numbers and percentages of species unique to each site, as well as those shared among the four sites, were also determined. Because only a few compendia on floras describe hybrids, it is exceedingly difficult to identify them, especially in the field. Hence,

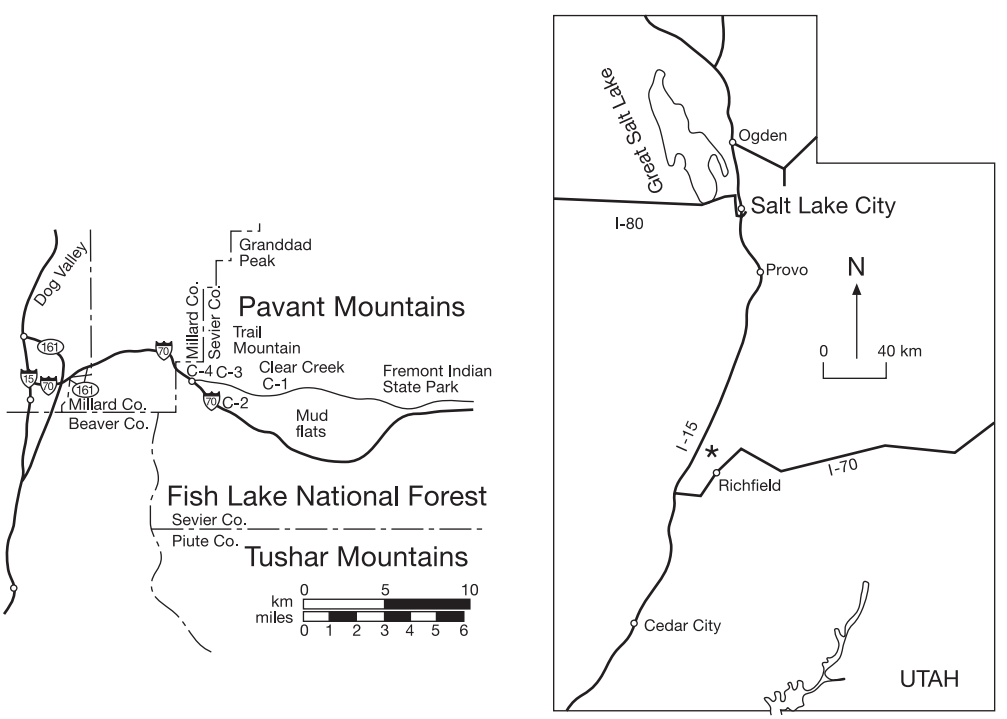

Fig. 1. A map of Clear Creek Canyon showing the four sites sample. C-1 is the basin habitat, C-2 and C-3 are in the hybrid zone and C-4 is the mountain habitat.

hybrids have rarely been taken into account in vegetation analysis (Knapp, 1984). The same methods that are applicable to species or other taxa can be used to treat hybrids in vegetation analysis. We identified hybrids based upon morphology (Freeman *et al.*, 1991) and treated hybrids as a separate taxon.

Demographic structure

Population densities of new recruits (1-year-old seedlings), small-, medium- and large-size big sagebrush (see Wang, 1996, for size criteria) were determined at each of the four sites, using 12 quadrats 10×10 m in size, at each site.

Data analysis

For the proportions of vegetation, litter, rock and bare ground cover, Bartlett's χ^2 for homogeneity of variance was used (Zar, 1984). If Bartlett's χ^2 test showed homoscedasticity ($P > 0.05$), a one-way analysis of variance and an *a posteriori* Student-Newman-Keuls test were conducted. In contrast, if Bartlett's χ^2 test indicated heteroscedasticity ($P < 0.05$), the data were log-transformed. In every case, the transformation resulted in homoscedasticity. Population density was analysed using a log-linear model (Norusis, 1988).

A canonical correspondence analysis of the community data and its ordination (Ter Braak, 1992) was performed to determine if the hybrid zone and two parental sites differ in community compositions. This analysis also allowed us to identify the environmental factors (soil depth, pH and elemental concentrations) that are associated with the hybrid zone and the parental sites.

RESULTS

Floristic analysis

In total, 77 species were encountered in the study. Thirty-two species are found at the basin site (C-1), 40 at the mountain site (C-4), and 26 and 30 at the two hybrid sites (C-2 and C-3, respectively). Floristically, all sites are remarkably dissimilar. We plotted the floristic similarity as the percentage of species that a site shares with each of the other sites (Fig. 2). Only 41% of the species found at the basin site also occur at the adjacent C-2 hybrid site. By comparison, 31% of the species found in the basin site also occur in the mountain site. Twenty-eight percent of the species found at the mountain site also occur in the adjacent C-3 hybrid site. The two hybrid zone sites are much more floristically similar to each other than they are to either parental site: 69% of the species found in C-2 also occur in C-3, and 56% of the species found in C-3 also occur in C-2. Each site also contains a number of unique species (C-1, 25%; C-2, 19%; C-3, 23%; C-4, 55%). The distribution of life form groups did not differ among sites ($\chi^2 = 6.40$, d.f. = 12, $P > 0.8$) (Fig. 3). The basin, mountain and C-2 hybrid sites all had four introduced species, whereas the C-3 hybrid site contained only two introduced species. Interestingly, only 5 of 77 species (*Alyssum desertorum*, *Bromus tectorum*, *Chrysothamnus viscidiflorus*, *Elymus elymoides* and *Eriogonum racemosum*) can be found in all four sites. Moreover, some species, such as *Descurainia pinnata*, occurred at both parental sites, but at neither hybrid site. The species diversity did not differ appreciably among the sites ($H'_{C\text{-}1} = 10.8$, $H'_{C\text{-}2} = 8.3$, $H'_{C\text{-}3} = 10.1$, $H'_{C\text{-}4} = 10.4$).

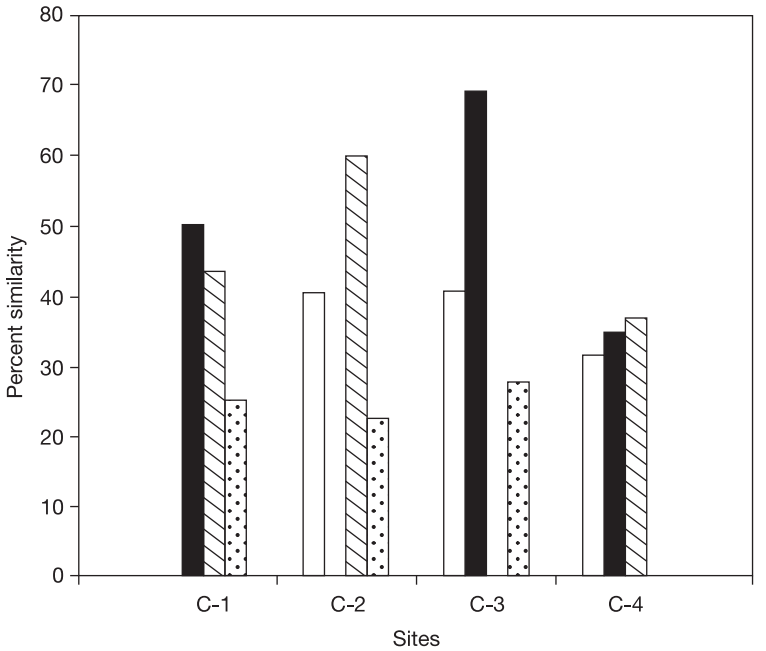

Fig. 2. Floristic similarity among the sites. The percent similarity was computed as the ratio of the number of species found at both sites divided by the number of species at the reference site. For example, 13 species occurred in both C-1 and C-2, while a total of 32 species occurred at C-1, so the percent similarity is $100 \times 13/32$. □, C-1; ■, C-2; ▨, C-3; ⊡, C-4.

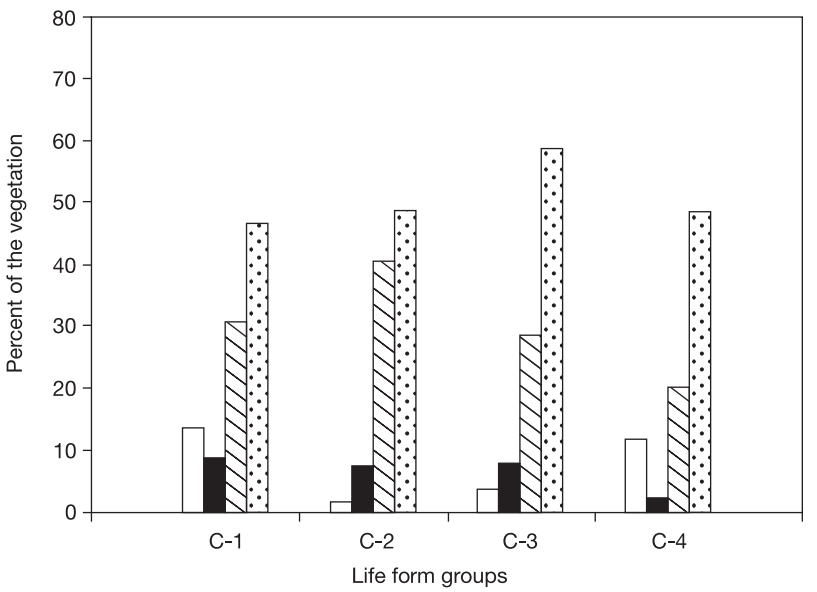

Fig. 3. The percentage of the vegetation in each life form group at the four sites. □, annuals; ■, forbs; ▨, gramenoids; ⊡, shrubs.

Vegetation analysis

The basin and two hybrid zone sites had significantly more vegetation and litter than the mountain site, whereas the mountain site had significantly more rock and bare ground than the basin and two hybrid zone sites (Table 1).

On a percentage basis, introduced species contributed between 4.7% (in the C-2 hybrid site) and 22.6% of the vegetation in the basin site ($F_{3,73} = 6.41$, $P < 0.001$). The C-2 hybrid site differed from all the other sites, but the other sites did not differ from one another (Fig. 4). Both the log of the percent annuals and the log of the percent forbs differed significantly among the sites ($F_{3,59} = 2.30$, $P < 0.0001$; $F_{3,59} = 1.73$, $P < 0.012$, respectively; Fig. 3). For the annuals, the two hybrid sites did not differ from each other, but the C-2 hybrid site had significantly less annual plant cover than either parental site. The C-3 hybrid site, however, did not differ from the mountain site, but did have significantly less annual plant cover than the basin site. The parental sites did not differ from each other. The basin site had a significantly higher percentage of forb cover than the mountain site, but neither parental site differed significantly from the two hybrid sites. No differences were observed for shrubs or grasses, and the sparse tree data were not analysed.

Community canonical correspondence analysis and ordination

The ordination based on canonical correspondence analysis showed that the basin site (C-1) is completely separated from the mountain site (C-4), with the two hybrid sites (C-2 and C-3) clustering into another separate group (Fig. 5). This suggests that the hybrid zone and two parental sites possess unambiguously distinct community compositions.

Table 1. Percentages of vegetation, litter, rock and bare ground in the four sites in Clear Creek Canyon, Richfield, Utah: Mean and standard deviation (in parentheses)

	Basin (C-1)	Near-basin (C-2)	Near-mountain (C-3)	Mountain (C-4)
Vegetation	66.3 ^{a,b} (19.7)	62.8 ^{a,b} (19.5)	75.8 ^{b} (16.0)	55.8 ^{a,b} (24.1)
Litter	89.3 ^{a} (14.0)	77.5 ^{c} (21.6)	78.3 ^{c} (19.8)	54.5 ^{b} (28.4)
Rock	1.1 ^{a} (2.1)	0.0 ^{a} (0.0)	0.0 ^{a} (0.0)	10.9 ^{b} (10.9)
Bare ground	7.8 ^{a} (11.3)	22.0 ^{b} (21.9)	21.5 ^{b} (19.8)	31.3 ^{b} (23.0)

Note: The vegetation percentage had a homogeneous variance (Bartlett $\chi^2_3 = 1.1$, $P = 0.38$); the litter, rock and bare ground percentages had heterogeneous variances (Bartlett $\chi^2_3 > 3.0$, $P < 0.05$). One-way analyses of variance showed that the vegetation percentage differed significantly among the four sites ($F_{3,76} = 3.45$, $P < 0.05$). Kruskal-Wallis tests showed that the litter, rock and bare ground percentages differed significantly among the four sites ($\chi^2_3 > 15.54$, $P < 0.01$). A sequential Bonferroni test (Rice, 1989) showed that the four parameters differed significantly among the four sites ($P < 0.05$). The results of both the Student-Newman-Keuls tests for the vegetation percentage and Kruskal-Wallis multiple comparison for the litter, rock and bare ground percentages are indicated by superscripts of the means: means with different superscripts differed significantly from one another ($P < 0.05$).

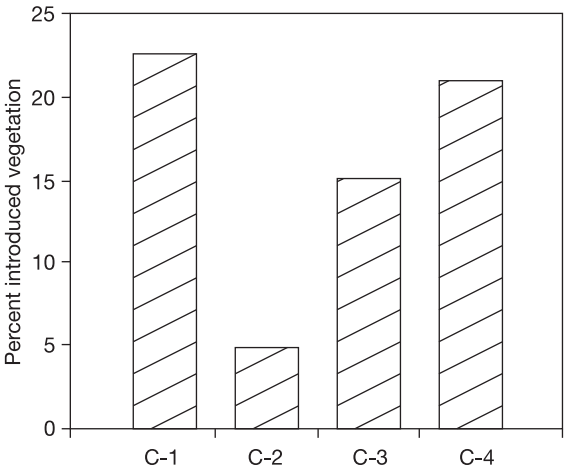

Fig. 4. The percentage of the vegetation introduced at the four sites.

Furthermore, the basin site has the deepest soil with the highest concentration of Mo (figure 5 and table 2 of Wang *et al*., 1998). At that site, *A. t.* ssp. *tridentata* is associated with *Eriogonum davidsonii*, *E. heracleoides*, *Gylcyrrhiza lepidota* and *Cryptantha* sp. (i.e. these species do not occur in C-2, C-3 and the mountain site; see Appendix). The mountain site has the soil with the highest concentrations of Fe and Se (figure 5 and table 2 of Wang *et al*., 1998). There, *A. t*. ssp. *vaseyana* is associated with *Pinus edulis*, *Elymus spicatum*, *E. intermedium* and *Purshi tridentata*. These species do not occur at the other three sites. The two hybrid sites have the soil with the highest concentrations of Na, Mg, Ca and K (figure 5 and table 2 of Wang *et al*., 1998). Hybrids are associated with *Lupinus sericeus*, *Juncus balticus*, *E. trachycaulum* and *E. smithii*. These species do not occur in either parental site. The hybrid sites are not well separated from each other, but, with the exception of one plant (possibly misclassified because our classification was based solely on morphology) from the basin site, are distinct from either parental site.

Demographic structure of the hybrid zone

The population densities of big sagebrush differed significantly among the four sites and size classes. There was also a significant site by size class interaction (Table 2). The density was significantly greater in the basin site ($Z = 3.37$, $P < 0.01$) and significantly lower in the mountain site ($Z = -3.04$, $P < 0.01$) than would be expected by random chance. The hybrid sites did not differ from random expectations. Density also varied significantly among the size classes. There were more small plants than would be expected by random chance ($Z = 8.43$, $P \ll 0.01$), and significantly fewer medium ($Z = -3.26$) and larger plants ($Z = -4.19$). The density of seedlings did not differ from random expectations. There was also a significant site by size interaction ($\chi^2 = 33.29$, $P < 0.001$). Seedlings and small plants both occur at greater densities in the basin site than at the other sites ($Z = 3.51$, $P < 0.01$; $Z = 3.16$, $P < 0.01$, respectively). There were significantly fewer seedlings in the mountain site than would be expected by chance ($Z = -3.56$, $P < 0.01$). No other cells differed

Table 2. Density of sagebrush by size in ten 10 m^2 plots at the four sites in Clear Creek Canyon, Richfield, Utah

	Basin (C-1)	Near-basin (C-2)	Near-mountain (C-3)	Mountain (C-4)
Seedlings	45	32	14	7
Small size	60	38	44	33
Medium size	20	11	14	17
Large size	14	15	24	18
Pooled	94	64	82	68

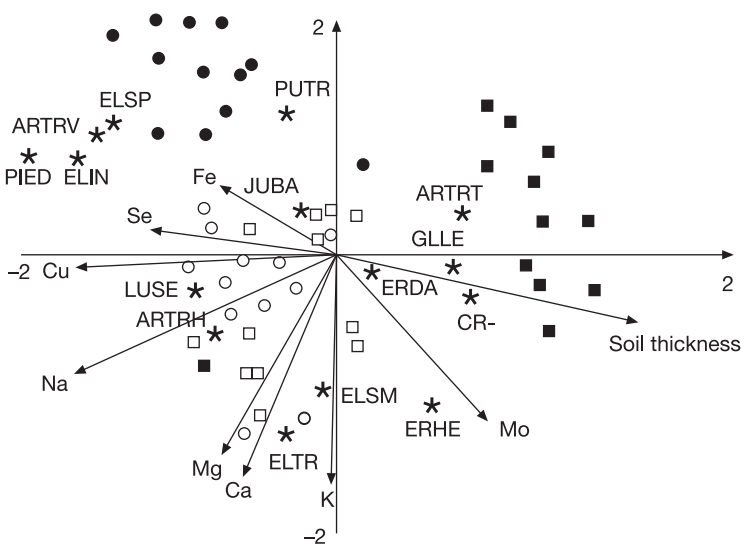

Fig. 5. Ordination based on canonical correspondence analysis of the community data with respect to the edaphic properties in Clear Creek Canyon, Richfield, Utah. ■, the basin site, C-1; ●, the mountain site, C-4; □ and ○, the two hybrid sites, C-2 and C-3, respectively. Species are indicated by asterisks. ARTRT = *Artemisia tridentata* ssp. *tridentata*, GLLE = *Glycyrrhiza lepidota*, ERDA = *Eriogonum davidsonii*, ERHE = *E. heracleoides*, CR- = *Cryptantha* sp. (all five found only at the basin site), JUBA = *Juncus balticus*, LUSE = *Lupinus sericeus*, ELTR = *Elymus trachycaulum* (all three found only at the near-basin site), ELSM = *Elymus smithii*, ARTRH = *A. t.* ssp. *tridentata* × *A. t.* ssp. *vaseyana* (both found at the near-basin and near-mountain sites only), ARTRV = *A. t*. ssp. *vaseyana*, PIED = *Pinus edulis*, PUTR = *Purshia tridentata*, ELSP = *Elymus spicatum*, ELIN = *Elymus intermedium* (all five found only at the mountain site). Arrows indicate edaphic properties. Only the 40 most common species were used for this analysis. A complete description of the soil data and analysis can be found in Wang *et al.* (1997, 1998).

significantly from random expectations. Thus the general pattern is that density is higher than expected in the basin zone, significantly lower than expected in the mountain zone, and random in the hybrid zone. Thus, there is no apparent population density trough in the hybrid zone.

DISCUSSION

Our results show that the big sagebrush hybrid zone occurs at an ecotone. More than 60% of the flora in either parental zone did not occur in the hybrid zone. The two hybrid sites are more similar floristically to each other than to the adjacent parental sites. The proportions of total vegetation, litter, rock and bare ground cover vary significantly among the sites. The big sagebrush subspecies and their hybrids each appear to be associated with corresponding groups of unique species. These results, coupled with edaphic heterogeneity (Wang *et al*., 1998), provide strong evidence for an abrupt discontinuity across the zone. Moreover, this discontinuity affects the distributions of the majority of species within the region. We find it most interesting that of the 77 species we encountered, only 5 were found at all four sites. Clearly, there is an abrupt discontinuity in the environment that affects the parental sagebrush taxa as well as the majority of other species.

An ecotone, by definition, is a transition region between two diverse communities, which shares some of the properties of each of those communities. Our results clearly show this to be the case at Clear Creek Canyon. We have suggested elsewhere that hybridization provides the genetic variance required for a species to occupy such sites with sharp ecological gradients (Wang *et al*., 1998).

Hybrid zones are believed to occur at ecotones or in disturbed habitats, although there is little direct evidence for either (for reviews, see Moore and Price, 1993; Arnold, 1997). Both ecotones and disturbed areas are places where communities change. Genetically compatible taxa may, therefore, occur in the proximity required to form hybrids in such environments. The prevailing impression is that competition is lower in ecotones or disturbed sites, making them ideal places for hybrids (which are presumed less fit) to become established (see Arnold, 1997). Our data do not support this presumption. Annual plants and introduced plants are generally more abundant in disturbed sites or sites with reduced competition. At Clear Creek Canyon, the hybrid sites had significantly less annual or introduced plant cover than one or both parental sites. Thus, the hybrid zone does *not* occur in an area of reduced competition. We find it interesting that native annuals, such as *Descuriania pinnata*, occur at both parental sites but at neither hybrid site. If the hybrid zone was highly disturbed, such opportunists should be more prevalent there, but our results contradict this expectation. Furthermore, controlled reciprocal transplant studies show that the hybrids are more fit than either parental taxon within the hybrid zone, but less fit outside the hybrid zone (Wang *et al*., 1997). All of our findings, to date, are in accordance with the bounded hybrid superiority model.

The premise underlying the dynamic equilibrium model is that hybrid unfitness results from the disruption of co-adapted gene complexes. Thus, the postulated equilibrium between selection and gene flow does not depend upon environmental factors. Furthermore, the zone is predicted to move until it encounters areas of low population density. This movement is a further indication of ecological neutrality. Our results do not support either this prediction or the assumption of hybrid unfitness. In an earlier paper (Freeman *et al*., 1995), we used measures of developmental instability to examine the disruption of co-adapted gene complexes. In contrast to the prediction of the dynamic equilibrium model, we found that the mountain taxon was the most developmentally unstable. Here we found no evidence for a population density trough in the big sagebrush hybrid zone in Clear Creek Canyon; to the contrary, the lowest density occurred in the parental mountain zone. Thus, our results consistently conflict with the predictions of the

dynamic equilibrium model, while affirming the predictions of the bounded hybrid superiority model.

Most of the sparse ecological work done to date on hybrid zones has been done with plants, or has examined the effect of plant hybridization on the associated animal taxa (for reviews, see Whitham, 1989; Whitham *et al.*, 1994, 1996). There has been very little work done on the ecology of animal hybrid zones (but see White and Chinnick, 1957; Howard, 1986; Kohlmann *et al.*, 1988; Nichols and Hewitt, 1988; Moore and Price, 1993). Such work could be useful in discriminating among the competing models, particularly given the difficulty of conducting reciprocal transplant experiments with animals.

Hybrid zones are areas of intense change in both genetic composition of the hybridizing taxa and the environment. Such sites provide a rich opportunity to explore the interactions between genetics and ecology at a variety of levels.

REFERENCES

Arnold, M.L. 1997. *Natural Hybridization and Evolution.* Oxford: Oxford University Press.

Axelrod, D.I. 1950. *The Evolution of Desert Vegetation in Western North America*. Publication 590. Washington, DC: Carnegie Institute.

Barton, N.H. 1983. Multilocus clines. *Evolution*, **37**: 454–471.

Barton, N.H. and Hewitt, G.M. 1985. Analysis of hybrid zones. *Ann. Rev. Ecol. Syst.*, **16**: 113–148.

Barton, N.H. and Hewitt, G.M. 1989. Adaptation, speciation and hybrid zones. *Nature*, **341**: 497–499.

Bazykin, A.D. 1969. Hypothetical mechanism of speciation. *Evolution*, **23**: 685–687.

Beetle, A.A. and Young, A. 1965. A third subspecies in the *Artemisia tridentata* complex. *Rhodora*, **67**: 405–406.

Briggs, D. and Walters, S.M. 1984. *Plant Variation and Evolution*, 2nd edn. Cambridge: Cambridge University Press.

Byrd, D.W. 1992. Biochemical assessment of the hybrid zone formed by *Artemisia tridentata tridentata* and *Artemisia tridentata vaseyana* using an automated gas chromatography-data system and statistical methods. Masters thesis, Wayne State University, Detroit, MI.

Byrd, D.W., McArthur, E.D., Wang, H., Graham, J.H. and Freeman, D.C. 1999. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): VIII. Spatial and temporal pattern of terpenes. *Biochem. Syst. Ecol.*, **27**: 11–25.

Clausen, J., Keck, D.D. and Hiesey, W.M. 1940. *Experimental Studies on the Nature of Species. I. Effects of Varied Environments on Western North American Plants.* Publication 520. Washington, DC: Carnegie Institute.

Cruzan, M.B. and Arnold, M.L. 1993. Ecological and genetic associations in an *Iris* hybrid zone. *Evolution*, **47**: 1432–1445.

Emms, S.K. and Arnold, M.L. 1997. The effects of habitat on parental and hybrid fitness: Transplant experiments with Louisiana irises. *Evolution*, **51**: 1112–1119.

Endler, J.A. 1977. *Geographic Variation, Speciation and Clines*. Princeton, NJ: Princeton University Press.

Freeman, D.C., Turner, W.A., McArthur, E.D. and Graham, J.H. 1991. Characterization of a narrow hybrid zone between two species of big sagebrush (*Artemisia tridentata*: Asteraceae). *Am. J. Bot.*, **78**: 805–815.

Freeman, D.C., Graham, J.H., Byrd, D.W., McArthur, E.D. and Turner, W.A. 1995. Characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): III. Developmental instability. *Am. J. Bot.*, **82**: 1144–1152.

Graham, J.H., Freeman, D.C. and McArthur, E.D. 1995. Characterization of a narrow hybrid zone between two subspecies of big sagebrush, *Artemisia tridentata* (Asteraceae): II. Selection gradients and hybrid fitness. *Am. J. Bot.*, **82**: 709–716.

Howard, D.J. 1986. A zone of overlap and hybridization between two ground cricket species. *Evolution*, **40**: 34–43.

Key, K.H.L. 1968. The concept of stasipatric speciation. *Syst. Zool.*, **17**: 14–22.

Knapp, R. 1984. Perspectives on species differentiation and on hybridization in vegetation analysis and in phytosociological releves. In *Sampling Methods and Taxon Analysis in Vegetation Science* (R. Knapp, ed.), pp. 23–24. Handbook of Vegetation Science, Part 4. The Hague: W. Junk.

Kohlmann, B., Nix, H. and Shaw, D.D. 1988. Environmental predictions and distributional limits of chromosomal taxa in the Australian grasshopper *Caledia captiva* (F.). *Oecologia*, **75**: 483–493.

Levin, D.A. and Schmidt, K.P. 1985. Dynamics of a hybrid zone in *Phlox*: An experimental demographic investigation. *Am. J. Bot.*, **72**: 1404–1409.

Ludwig, J.A. and Reynolds, J.F. 1988. *Statistical Ecology*. New York: John Wiley.

McArthur, E.D. 1994. Ecology distribution and values of sagebrush within the intermountain region. In *Proceedings on Ecology and Management of Annual Rangelands* (compiled by S.B. Monsen and S.G. Kitchen), pp. 347–351. General Technical Report INT-GTR-313. Ogden, UT: USDA Forest Service, Intermountain Research Station.

McArthur, E.D. and Sanderson, S.C. submitted. Cytogeogeography and chromosome evolution of subgenus *Tridentatae* of *Artemisia*. *Am. J. Bot.*

McArthur, E.D., Pope, C.L. and Freeman, D.C. 1981. Chromosomal studies of subgenus *Tridentatae* of *Artemisia*: Evidence for autopolyploidy. *Am. J. Bot.*, **68**: 589–605.

McArthur, E.D., Welch, B.L. and Sanderson, S.C. 1988. Natural and artificial hybridization between big sagebrush (*Artemisia tridentata*) subspecies. *J. Heredity*, **79**: 268–276.

McArthur, E.D., Mudge, J.E., Van Buren, R., Anderson, W.R., Sanderson, S.C. and Babbel D.G. 1998a. Random amplified polymorphic DNA analysis (RAPD) of *Artemisia* subgenus *Tridentatae* species and hybrids. *Great Basin Nat*., **58**: 12–27.

McArthur, E.D., Freeman, D.C., Graham, J.H., Wang, H., Sanderson, S.C., Monoco, T.A. and Smith, B.N. 1998b. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): IV. Respiration and water potential. *Can. J. Bot*., **76**: 567–574.

Moore, W.S. 1977. An evaluation of narrow hybrid zones in vertebrates. *Quart. Rev. Biol.*, **52**: 263–277.

Moore, W.S. and Price, J.T. 1993. Nature of selection in the northern flicker hybrid zone and its implications for speciation theory. In *Hybrid Zones and the Evolutionary Process* (R.G. Harrison, ed.), pp. 196–225. Oxford: Oxford University Press.

Nichols, R.A. and Hewitt, D.M. 1988. Genetical and ecological differentiation across a hybrid zone. *Ecol. Entomol.*, **13**: 39–40.

Norusis, M.J. 1988. *SPSS/PC+ V2.0. Base Manual*: *Advanced Statistics*. Chicago, IL: SPSS Inc.

Potts, B.M. and Reid, J.B. 1985. Analysis of a hybrid swarm between *Eucalyptus risdonii* Hook and *E. amygdalina* Labill. *Aust. J. Bot*., **33**: 543–562.

Reiseberg, L.H. and Ellstrand, N.C. 1993. What can molecular and morphological markers tell us about plant hybridization? *Crit. Rev. Plant Sci*., **12**: 213–241.

Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**: 223–225.

Rosentreter, R. and Kelsey, R.G. 1991. Xeric big sagebrush, a new subspecies in the *Artemisia tridentata* complex. *J. Range Manage.*, **44**: 330–335.

Schmidt, K.P. and Levin, D.A. 1985. The comparative demography of reciprocally sown populations of *Phlox drummondii* Hook. I. Survivorships, fecundities, and finite rates of increase. *Evolution*, **39**: 396–404.

Stebbins, G.L. 1971. *Chromosomal Evolution in Higher Plants*. Reading, MA: Addison-Wesley.

Ter Braak, C.J.F. 1992. *CANOCO – A FORTRAN Program for Canonical Community Ordination*. Ithaca, NY: Microcomputer Power.

Wagstaff, F.J. and Welch, B.L. 1990. Rejuvenation of mountain big sagebrush on mule deer winter ranges using on-site plants as a seed source. In *Proceedings of a Symposium on Cheatgrass*

Invasion, *Shrub Die-off and Other Aspects of Shrub Biology and Management* (E.D. McArthur, E.M. Romney, S.D. Smith and P.T. Tueller, eds). General Technical Report INT-276. Ogden, UT: USDA Forest Service, Intermountain Research Station.

Wang, H. 1996. Ecological analysis of a stable hybrid zone between two big sagebrush species (*Artemisia tridentata* ssp. *tridentata* and *A. t.* ssp. *vaseyana*). PhD dissertation, Wayne State University, Detroit, MI.

Wang, H., McArthur, E.D., Sanderson, S.C., Graham, J.H. and Freeman, D.C. 1997. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): III. Reciprocal transplant experiments. *Evolution*, **51**: 95–102.

Wang, H., Byrd, D.W., Howard, J.L., McArthur, E.D., Graham, J.H. and Freeman, D.C. 1998. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). V. Edaphic properties. *Int. J. Plant Sci.*, **159**: 139–147.

Wang, H., McArthur, E.D. and Freeman, D.C. in press. Characterization of a narrow hybrid zone between two subspecies of big sagebrush, *Artemisia tridenteta* (Asteraceae): VI. Mineral uptake. *Am. J. Bot*.

Weber, D.J., Gang, D.R., Halls, S.C., Smith, B.N. and McArthur, E.D. 1994. Inheritance of hydrocarbons in subspecific big sagebrush (*Artemisia tridentata*) hybrids. *Biochem. Syst. Ecol.*, **22**: 689–697.

White, M.J.D. and Chinnick, L.J. 1957. Cytogenetics of the grasshopper *Moraba scurra*. III. Distribution of the 15 and 17 chromosome races. *Aust. J. Zool.*, **5**: 338–347.

Whitham, T.G. 1989. Plant hybrid zones as sinks for pests. *Science*, **244**: 1490–1493.

Whitham, T.G., Morrow, P.A. and Potts, B.M. 1994. Plant hybrid zones as centers for biodiversity: The herbivore community of two endemic Tasmanian eucalypts. *Oecologia*, **97**: 481–490.

Whitham, T.G., Floate, K.D., Martinsen, G.D., Dreibe, E.M. and Keim, P. 1996. Ecological and evolutionary implications of hybridization: Populus–herbivore interactions. In *Biology of Populus and Its Implications of Management and Conservation* (R.F. Stettler, H.D. Bradshaw, Jr., P.E. Heilman and T.M. Hinckley, eds), pp. 247–275. Ottawa: NRC Research Press.

Zar, J.H. 1984. *Biostatistical Analysis*, 2nd edn. Engelwood Cliffs, NJ: Prentice-Hall.

Appendix

Plants found in the four sampling sites in Clear Creek Canyon, Utah

Family	Genus	Species	Geographical origin	Site
Anacardiaceae	*Rhus*	*R. trilobata*	Native	C-1
Asteraceae	*Achillea*	*A. millefolium*	Native	C-3
	Agoseris	*A. glauca*	Native	C-4
	Artemisia	*A. carruthii*	Native	C-2, C-3, C-4
		A. ludoviciana	Native	C-4
		A. t. ssp. *tridentata*	Native	C-1
		A. t. ssp. *vaseyana*	Native	C-4
		A. t. ssp. *tridentata* × *A. t.* ssp. *vaseyana*	Native	C-2, C-3
		A. t. ssp. *wyomingensis*		
	Balsamorhiza	*B. sagittata*	Native	C-1, C-4
	Chaenactis	*C. douglasii*	Native	C-3, C-4
	Chrysothamnus	*C. nauseosus*	Native	C-1, C-2, C-3
		C. parryi	Native	C-2, C-3, C-4
		C. viscidiflorus	Native	C-1, C-2, C-3, C-4

Appendix *continued*

Family	Genus	Species	Geographical origin	Site
	Cirsium	*C.* sp.	Unknown	C-4
	Iva	*I. aillaris*	Native	C-2, C-3
	Senecio	*S. crassulus*	Native	C-2
		S. multilobatus	Native	C-3
	Taraxacum	*T. officinalis*	Native	C-2, C-4
	Viguiera	*V. multiflora*	Native	C-4
Berberidaceae	*Mahonia*	*M. repens*	Native	C-1, C-4
Boraginaceae	*Lithaspermum*	*L. ruderale*	Native	C-4
	Cryptantha	*C.* sp.	Unknown	C-1
Brassicaceae	*Arabis*	*A. perennans*	Unknown	C-4
	Cardaria	*C. draba*	Native	C-1, C-2
	Chorispora	*C. tenella*	Native	C-2
	Descurainia	*D. pinnata*	Native	C-1, C-4
	Lepidium	*L. virginicum*	Native	C-1, C-2, C-4
Cactaceae	*Opuntia*	*O. erinacea*	Native	C-1, C-4
		O. polyacantha	Native	C-3
Chenopodiaceae	*Chenopodium*	*C. fremontii*	Native	C-1, C-3
		C. leptophyllum	Native	C-1, C-4
Cupressaceae	*Juniperus*	*J. osteosperma*	Native	C-2, C-3, C-4
Liliaceae	*Allium*	*A.* sp.	Native	C-4
	Calochortus	*C. nuttallii*	Native	C-4
Luguminosae	*Astragalus*	*A. utanhensis*	Native	C-4
	Glycyrrhiza	*G. lepidota*	Native	C-1
	Lupinus	*L. sericeus*	Native	C-2
		L. sp.	Native	C-3
	Oxytropis	*O.* sp.	Native	C-4
	Quercus	*Q. gambelii*	Native	C-4
	Trifolium	*T. hybridium*	Native	C-3, C-4
Juncaceae	*Juncus*	*J. balticus*	Native	C-2
Onagraceae	*Gayopytum*	*G. ramosissimum*	Native	C-1, C-2, C-3
	Epilobium	*E.* sp.	Native	C-4
Orobanchaceae	*Orobanche*	*O. fasiculata*	Native	C-3, C-4
Pinaceae	*Pinus*	*P. edulis*	Native	C-4
Poaceae	*Elymus*	*E. intermedium*	Introduced	C-4
		E. smithii	Native	C-2, C-3
		E. spicatum	Native	C-4
		E. trachycaulum	Native	C-2
	Bromus	*B. tectorum*	Introduced	C-1, C-2, C-3, C-4
		B. inermis	Introduced	C-4
	Bouteloua	*B. gracilis*	Native	C-1, C-4
	Elymus	*E. cinereus*	Native	C-2, C-3
	Poa	*P. fendleriana*	Native	C-1
		P. praetensis	Introduced	C-1, C-2, C-3
		P. secunda	Unknown	C-2
	Sitanion	*S. hysterix*	Native	C-1, C-2, C-3, C-4
	Stipa	*S. hymenmoides*	Native	C-4

Appendix *continued*

Family	Genus	Species	Geographical origin	Site
Polemoniaceae	*Collomia*	*C. linearis*	Native	C-4
	Gilia	*G. inconspicua*	Native	C-4
	Microsteris	*M. gracilis*	Native	C-3, C-4
	Phlox	*P. longofolia*	Native	C-3
		P. sp.	Native	C-3
Polygonaceae	*Eriogonum*	*E. davidsonii*	Unknown	C-1
		E. heracleoides	Unknown	C-1
		E. racemosum	Unknown	C-1, C-2, C-3, C-4
	Polygonum	*P. douglasii*	Native	C-4
Ranunculaceae	*Ranunculus*	*R. testiculatas*	Native	C-4
Roseaceae	*Rosa*	*R. woodsii*	Native	C-1, C-3
	Purshia	*P. tridentata*	Native	C-4
Santalaceae	*Comandra*	*C. umbellata*	Native	C-4
Scropulariaceae	*Castilleja*	*C. linariifolia*	Native	C-1, C-2
	Penstemon	*P. comarrhenus*	Unknown	C-1, C-3
Selaginellaceae	*Selaginella*	*S. watsonii*	Unknown	C-1, C-2, C-3
Urticaceae	*Urtica*	*U. dioica*	Native	C-1
Violaceae	*Viola*	*V. nutfallii*	Native	C-2, C-3, C-4