

Use of Distance Measures to Assess Environmental and Genetic Variability Across Sagebrush Hybrid Zones

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Abstract—Reciprocal transplant studies in the big sagebrush hybrid zone at Salt Creek Canyon, Utah, showed that hybrids between basin (*Artemisia tridentata* ssp. *tridentata*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*) are more fit than either parental taxon, but only when raised in the hybrid zone. Hybrids are less fit than the native parent when raised in the parental environments. Why this is the case remains an open question. Our earlier work has shown that the hybrid zone occurs in an ecotone where the soil, vegetation, and herbivorous insect community all differ markedly from that found in the parental habitats. Moreover, the spatial variation in soil chemistry was greater in the hybrid zone than in either parental habitat. Does the enhanced genetic variation that results from hybridization allow hybrids to adapt to hyperspatial variability within the hybrid zone? Here we used Euclidean distance measures to examine this question for sagebrush hybrid zones found at Salt Creek and Clear Creek Canyons in Utah. Specifically, we examine the spatial variation in soil chemistry, vegetation, and insect communities. We also explore the interplant variability in the production of terpenes, ten elemental leaf concentrations, and the plants' biological absorption coefficients. While the hybrid zone is spatially more variable for soil chemistry, it is not more variable in terms of the vegetation nor herbivorous insects. Spatial variation for these features of the environment was greatest in the mountain zone, least in the basin zone and intermediate in the hybrid zone. In all three gardens overall, hybrid plants displayed greater variation than either parental taxon, in terms of their leaf elemental chemistry and biological absorption coefficients. However, the variability for all parental and hybrid plants increased when raised in alien gardens.

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Introduction

The bounded hybrid superiority model postulates that the maintenance of stable hybrid zones is due to genotype-by-environment interactions. Accordingly, the parental taxa and hybrids each have superior fitness in their native habitats. Hybrids are presumed to be more fit within the hybrid zone, but less fit outside it, compared to either parental taxon. Reciprocal transplant experiments are required to test this model, as descriptive studies or single common-garden experiments confound genetic and environmental effects, thereby preventing assessment of genotype-by-environment interactions. Recently, a number of reciprocal transplant experiments have been conducted with plants (Young 1996; Wang and others 1997; Emms and Arnold 1997). These studies found that the fitness of hybrids was generally equal or superior to that of the parental taxa within the hybrid zone, but less fit than either parental type outside the hybrid zone. This was most evident when estimates were made using composite fitness parameters (Wang and others 1997).

Why should superiority of hybrid fitness be confined to within the margins of the hybrid zone? As Kettlewell (1956) demonstrated, fitness can be a function of both genotype and the environment, so the above question actually comprises three different questions: (1) what is special about the environment of the hybrid zone? (2) why should hybrids exhibit superior fitness in this unique environment compared to the parental taxa? and (3) why can't hybrids expand their range and thereby displace the parental taxa?

While considerable attention has been given to the genetic analysis of hybrid zones (see Arnold 1997 for an excellent review), ecological analyses have received much less attention. Most ecological work has focused on the influence of plant hybrid zones on herbivore distribution and abundance (Whitham and others 1999; Pilon 1999; Moula 1999; Fritz 1999, and references therein). These studies are fascinating, but they do not address the issues raised here because the environment is not examined from a plant's perspective.

We have adopted an ecological approach to our study of the big sagebrush hybrid zone. A number of features relevant to the performance of plants (in other words, soil mineral composition and the distribution and abundance of other

Table 1—Sources of data used in this paper.

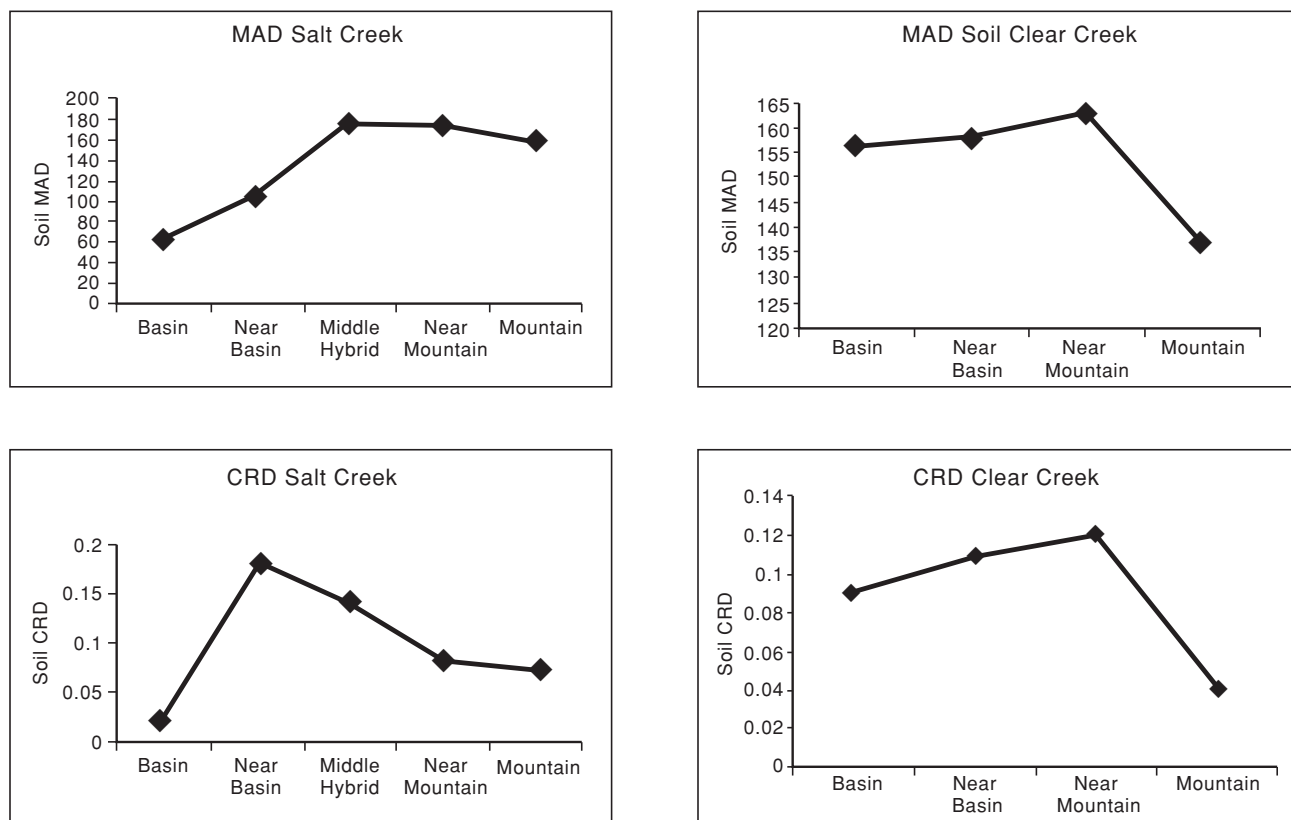
Insect Community Composition	Graham and others, 2001; Graham and others, this proceedings
Plant Chemistry	Wang and others 1999
Plant Community Composition	Freeman and others 1999
Plant Developmental Instability	Freeman and others 1995
Plant Terpenes	Byrd and others 1999
Soil Chemistry	Wang and others 1998

plant species and herbivorous insects) have been investigated (table 1). Profiles of defensive chemicals produced by the plants have also been examined. Thus far, these studies have supplied partial answers to the above three questions.

We have shown that the hybrid zone occurs in an ecotone. Specifically: (1) soil chemistry differs radically between the parental sites and parental habitat soils differ markedly from that of the hybrid zone; (2) soils from the hybrid zone are not just intermediate blends of the parental habitat soils, but have their own unique properties; (3) plant species composition and vegetation (estimated as percent of ground cover) differ significantly between the parental sites and these sites also differ from the hybrid zone; and (4) vegetation in the hybrid zone community is not a simple blend of that in the parental communities, but rather includes some unique species. In short, both soil chemistry and vegetation have unique features in the hybrid zone, to which the hybrids have adapted. However, hybrids are maladapted to the environmental conditions

existing in either parental zone (Wang and others 1997). Why hybrids, and not the parental taxa, are adapted to the unique features of the hybrid zone (question 2) remains open.

In an earlier paper (Wang and others 1998), Euclidean distance measures showed that the big sagebrush hybrid zone is spatially more variable in soil elemental composition than either parental site (fig. 1). This suggests that the enhanced genetic variation resulting from hybridization may be necessary to cope with the increased spatial variation of soil chemistry within the hybrid zone. The present study extends that analysis to examine the variability in vegetation, insect herbivore loads, and terpene profiles of leaves. Interplant variability is also examined for plants raised in common gardens, using elemental leaf concentrations and the ratio of elemental leaf to soil concentrations (in other words, the biological absorption coefficients, BACs). This latter analysis examines how the variability among plants changes when the plant is raised in a nonnative environment.

**Figure 1**—MAD and CRD distances based upon soil chemistry for both the Salt Creek and Clear Creek hybrid zones.

Methods

Methods for a specific data collection are given in the primary article dealing with that subject (table 1). We have primarily conducted our studies in Utah at both Salt Creek and Clear Creek Canyons. Salt Creek Canyon is located at the south end of the Wasatch Mountains near Nephi, whereas Clear Creek Canyon is located near Richfield and drains the east slope of the Pavant and Tushar Mountains. Sampling in both study areas occurred across the hybrid zone in native vegetation; however, data was also collected from three experimental gardens established in Salt Creek Canyon (one in each parental population and one in the middle of the hybrid zone—see Wang 1996). In the native vegetation at Salt Creek Canyon, five sampling sites were established (one in each parental population and three within the hybrid zone), while four were established at Clear Creek Canyon (one in each parental population and two within the hybrid zone). Soil chemistry was assessed at both sites, whereas vegetation was only assessed at Clear Creek Canyon because portions of Salt Creek Canyon have been seeded with alien grasses. Cattle grazing occurs at both locations. Terpene profiles and insect abundance were analyzed for transplant-garden plants at Salt Creek Canyon. Leaf chemistry was also addressed using plants indigenous to a site.

Euclidean distance was used to measure spatial environmental heterogeneity. Specifically, to examine differences due to magnitudes, the mean absolute Euclidean distance (MAD) was determined by applying the following equation (Freeman and others 1995):

$$\text{MAD} = S \sum_{j=1}^S \sum_{k=1}^S X_{ij} - X_{ik} / S$$

Using soil chemistry as an example, X_{ij} is the measure of the magnitude of the i^{th} element in sample j , X_{ik} represents the concentration of the same element in sample k , and S represents the number of elements included in the distance estimate. We measured the concentrations of 10 elements in the soil, so, in this case, $S = 10$. The concentration of each element forms an axis in the analysis, and the distance between the samples is a measure of their dissimilarity. This distance is summed for each axis and then divided by the number of elements to yield the MAD estimate. Chord distance (CRD) is similar, but examines proportions rather than absolute amounts:

$$\text{CRD} = s \cdot 2(1 - \text{ccos}_{jk})$$

where

$$\text{ccos}_{jk} = S \sum_{i=1}^S (X_{ij} - X_{ik})^2 / S^2$$

$$s = \sqrt{2/S}$$

In brief, the distance between samples is projected onto a unit circle and the chord that separates the two samples is a measure of the dissimilarity in the proportion of elements

measured in the soils. Vegetation, terpenes and leaf chemistry were treated in a similar manner.

Data Analysis

When analyzing the distances for vegetation, terpenes, and herbivore loads, a Kruskal-Wallis test was used because the data did not conform to the assumptions of an ANOVA (Zar 1984). However, ANOVAs were used to analyze elemental leaf concentrations and their biological absorption coefficients.

Results

Soil Chemistry

Soil chemistry plays such an important role in the present study that we will summarize the results of Wang and others (1998). Both MAD and CRD distances differed significantly among the sites at Salt Creek Canyon ($\chi^2 > 40.0$, $P < 0.00001$ in both cases) (fig. 1). MAD distances at the basin site were significantly less than at the middle-hybrid site, but not at the near-basin or mountain sites. The near-basin and mountain sites did not differ significantly from the middle hybrid or near-mountain sites. CRD distances differed significantly between the basin and four other sites at Salt Creek Canyon. At Clear Creek Canyon, MADs did not differ among the sites, but CRDs did ($\chi^2 > 40.0$). The mean CRD at the mountain site was significantly less than at the other three sites, while the mean CRD at the near-mountain site was significantly greater than the means at either the basin or near-basin site. This indicates that at Salt Creek Canyon, both the concentrations and proportions of elements in the soils were spatially more variable in the hybrid zone than at the basin site. While the spatial variability was greater in the hybrid zone than at the mountain site, the difference was not significant. At Clear Creek Canyon, the spatial variation in the proportion of elements was greater in the hybrid zone than at the mountain site.

Vegetation

MADs differed significantly among the sites ($\chi^2 = 23.4$, $P < 0.000034$, table 2). Mean MAD at the basin site was significantly greater than at the other three sites, while these sites did not differ from one another. This indicates that quadrats in the basin site had greater disparity in the amount of vegetation than that occurring at the other sites. CRD distance also differed significantly among the sites ($\chi^2 = 135.0$, $P < 0.000001$). The mean CRD at the basin site was significantly less than that at the near-basin and mountain sites, but did not differ from that at the near-mountain

Table 2—Analysis of spatial heterogeneity of the vegetation using Euclidean distance measures at the Clear Creek Site. The MAD examines differences among quadrats in the amount of vegetation while the CRD examines differences in the proportion of vegetation contributed by each species. Means subscripted by the same letter do not differ significantly from one another at the 0.05 level.

	Basin	Near basin	Near mountain	Mountain	χ^2	P
MAD	2.21 _a	1.75 _b	1.88 _b	1.85 _b	23.37	0.000034
CRD	0.96 _a	1.05 _b	0.94 _a	1.25 _c	134.99	0.000001

Table 3—Analysis of spatial heterogeneity of the insect community using Euclidean distance measures at the Clear Creek Site. The MAD examines differences among plants in the number of insects while the CRD examines differences in the proportion of individuals contributed by each species. Means subscripted by the same letter do not differ significantly from one another at the 0.05 level.

Garden	Source	MAD	CRD
Basin	Basin	7.39 _c	0.16 _a
Basin	Near Basin	12.36 _d	0.54 _b
Basin	Middle Hybrid	12.41 _d	0.25 _a
Basin	Near Mountain	13.78 _d	0.19 _a
Basin	Mountain	15.05 _d	0.35 _a
Hybrid	Basin	6.31 _c	0.30 _a
Hybrid	Near Basin	7.10 _c	0.55 _b
Hybrid	Middle Hybrid	3.09 _b	0.57 _b
Hybrid	Near Mountain	5.52 _b	0.25 _a
Hybrid	Mountain	3.07 _b	0.57 _b
Mountain	Basin	0.67 _a	1.04 _c
Mountain	Near Basin	0.85 _a	0.98 _c
Mountain	Middle Hybrid	1.61 _a	0.58 _b
Mountain	Near Mountain	1.54 _a	0.98 _c
Mountain	Mountain	0.38 _a	1.07 _c

site. Mean CRD at the near-basin site was significantly greater than that at the near-mountain site, but significantly less than that at the mountain site. Mean CRD at the mountain site was significantly greater than that at the other three sites. Collectively, these results indicate that the proportion of vegetation contributed by a species was remarkably uniform at the basin site, but that the density of vegetation there varied greatly among the quadrats. While at the mountain site, the amount of vegetation was quite constant but the composition of the vegetation varied greatly among the quadrats. Thus, by either measure, the **parental sites are more variable** than either hybrid site.

Insects

MADs were examined for plants in the common gardens. The data were not normally distributed, so a Kruskal-Wallis test was used for this analysis. A single coding variable was also used to indicate both garden and source populations (table 3). As there are three gardens and five source populations, this coding variable had 15 states. MADs differed significantly among these 15 states ($\chi^2=571.9, P<0.000001$). In general, two major trends are evident: (1) the site-indigenous population always had the smallest MAD and (2) hybrids had greater MADs than the parental taxa (this trend is more evident in the parental gardens, though the nonindigenous hybrids had higher MADs even in the hybrid

garden). The mean CRDs also varied significantly among the 15 states of the coding variable ($\chi^2=214.4, P<0.000001$). In general, the mean CRD was lowest in the basin garden and highest in the mountain garden, with basin plants having lower CRDs than mountain plants. One form of hybrid had the highest CRDs in the basin and hybrid gardens, but not in the mountain garden where mountain plants had the highest CRD. Thus, the total density of insects appears to be most variable on the nonsite indigenous and hybrid plants. Like the vegetation, the proportional contribution of an insect species to the total herbivore load was more uniform in the basin than mountain garden. In the basin and middle-hybrid gardens the proportions of insect species varied most among the hybrids, but in the mountain garden, native parental plants had greater variability.

Terpenes

MADs differed significantly among the five sampling locations at Salt Creek Canyon ($\chi^2=42.8, P<0.000001$) (table 4). Mean MAD at the basin site was significantly less than that at the near-mountain and mountain sites. No other differences were significant. CRDs did not differ among the sites ($\chi^2=0.4, P=n.s.$).

Leaf Chemistry

Site Indigenous Plants—Leaf chemistry was examined for both site-indigenous and transplant-garden plants. For site-indigenous plants, MADs were significantly greater for the basin and middle-hybrid plants than for the mountain and near-basin plants. Near-mountain plants were intermediate (table 5). CRDs also differed significantly among the sites ($F_{4,135}=4.19, P<0.003$, table 5 and fig. 2). CRDs were greatest for the middle-hybrid and basin plants and lowest for near-basin and mountain plants. MADs based on the biological absorption coefficient also differed significantly among the sites, ($F_{4,135}=12.48, P<0.001$, table 5), being significantly higher for basin plants than for any hybrid or mountain plants. Mountain plants had the lowest MAD distances. Similarly, CRDs varied among the sites ($F_{4,135}=2.73, P<0.03$, table 5) and were highest for the near-mountain plants and lowest for the middle-hybrid plants.

Transplant Gardens

Elemental Concentrations—MADs based upon elemental concentrations differed significantly among the gardens ($F_{2,210}=7.195, P<0.001$). The mountain garden had the lowest MADs, which differed significantly from those in the

Table 4—Analysis of the spatial heterogeneity of terpenes produced by plants at Salt Creek Canyon. The MAD examines differences among plants in the quantities of terpenes produced while the CRD examines differences in the proportion of terpenes produced. Means subscripted by the same letter do not differ at the 0.05 level.

	Basin	Near basin	Middle hybrid	Near mountain	Mountain	χ^2	P
MAD	0.41 _a	0.45 _a	0.47 _a	0.87 _b	0.74 _b	42.8	0.000001
CRD	1.37	1.37	1.37	1.35	1.34	0.4	N. S.

Table 5—An analysis of the spatial heterogeneity among plants in concentrations of 10 elements in leaf tissue. The MAD distance examines the concentrations of the elements; the CRD distance examines the proportions of elements. Both site-indigenous and reciprocally transplanted individuals were examined. Means subscripted by the same letter do not differ at 0.05 level.

Elemental concentrations	Site-indigenous plants					F(4,135)	P
	Basin	Near basin	Middle hybrid	Near mountain	Mountain		
MAD	526.57 _a	294.28 _b	542.72 _a	400.44 _{ab}	312.68 _b	6.14	0.001
CRD	0.15 _{ab}	0.09 _a	0.18 _b	0.13 _{ab}	0.1 _a	4.19	0.003
Biological absorption coefficient							
MAD	10.14 _a	6.37 _b	6.95 _b	5.71 _b	3.2 _c	12.48	0.001
CRD	0.09 _{ab}	0.07 _{ab}	0.06 _a	0.10 _b	0.09 _{ab}	2.73	0.03

basin and hybrid gardens; the MADs for these latter two gardens did not differ from one another. MADs also differed significantly among source populations ($F_{4,210} = 3.231$, $P < 0.013$, table 6). The near-basin plants had the largest MADs, which differed from the MADs of the basin and near-mountain plants, but not the middle-hybrid or mountain plants. There was no difference among the gardens and the interaction term was not significant. CRDs differed significantly among the source populations ($F_{4,210} = 3.955$, $P < 0.004$, table 6), but not among the gardens. The mean CRD distance was significantly greater among the mountain plants than among the basin, near-mountain and middle-hybrid plants. The mean CRD among near-basin plants was intermediate. The garden-by-source population interaction was marginally significant ($F_{8,210} = 1.93$, $P < 0.058$, table 7).

Biological Absorption Coefficients

MADs distances among plants showed the following significant trend: basin garden > middle hybrid garden > mountain garden ($F_{2,210} = 27.003$, $P < 0.001$). MADs also varied

significantly among the source populations ($F_{4,210} = 4.001$, $P < 0.004$, table 6). MADs were greatest among the middle hybrids, and least among near-mountain hybrids. The other source populations were intermediate and did not differ from each other, the middle-hybrid or near-mountain plants. The interaction among gardens and source populations was also significant, ($F_{8,210} = 4.563$, $P < 0.001$, table 6 and fig. 2). As a general rule, site-indigenous plants had the lowest MADs, while nonindigenous parental plants and at least one type of hybrid had the greatest MADs.

CRDs showed the following significant trend: mountain garden > basin garden > middle-hybrid garden ($F_{2,210} = 48.070$, $P < 0.001$). CRDs also varied significantly among the source population ($F_{4,210} = 9.210$, $P < 0.000$, table 6 and fig. 2). CRDs were significantly greater for middle hybrid and basin plants than for mountain and near-mountain plants. Near-basin plants were intermediate. The interaction between garden and source population was also significant ($F_{8,210} = 3.420$, $P < 0.001$, table 6). In general, CRDs were greatest for hybrid and basin plants and lowest for mountain plants; however, relative ranking among the different hybrid sources varied among the gardens.

Table 6—An analysis of the spatial heterogeneity in the concentrations of elements and the biological absorption coefficients among plants in the transplant gardens at Salt Creek Canyon. The MAD distance examines heterogeneity in the concentrations of elements while the CRD distance examines differences in the proportions of the elements.

Elemental concentration		Source population				
		Basin	Near basin	Middle hybrid	Near mountain	Mountain
Garden						
MAD	Basin	560.77 _a	808.16 _b	593.87 _a	533.63 _a	824.88 _b
MAD	Hybrid	628.41	779.26	711.44	624.7	729.87
MAD	Mountain	509.6	629.93	590.22	463.27	426.23
CRD	Basin	0.16 _{ab}	0.19 _{ab}	0.12 _{ab}	0.09 _a	0.21 _b
CRD	Hybrid	0.1 _a	0.17 _{ab}	0.11 _a	0.18 _{ab}	0.22 _b
CRD	Mountain	0.14	0.14	0.16	0.13	0.16
Biological absorption coefficients						
MAD	Basin	75.42 _a	100.85 _{ab}	81.75 _a	74 _a	107 _b
MAD	Hybrid	65.16	48.66	62.56	53.85	47.45
MAD	Mountain	59.66 _a	63.5 _a	84.71 _a	25.11 _b	27.03 _b
CRD	Basin	0.19 _a	0.13 _{ab}	0.15 _{ab}	0.09 _b	0.12 _{ab}
CRD	Hybrid	0.09	0.07	0.1	0.07	0.05
CRD	Mountain	0.2 _{ab}	0.26 _{bc}	0.31 _c	0.15 _a	0.12 _a

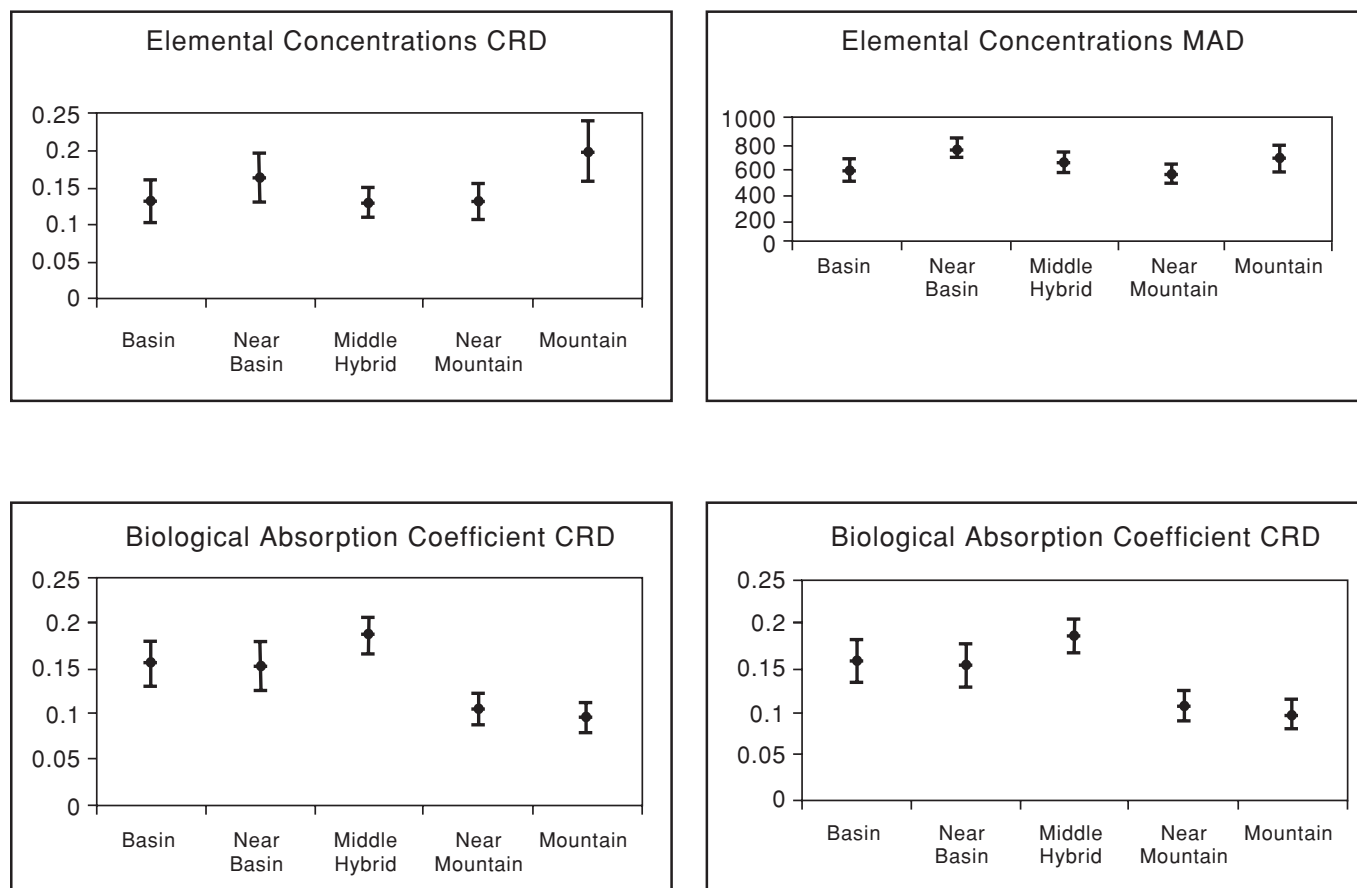


Figure 2—Comparison of MAD and CRD distances based upon plant chemistry among the five source populations.

Discussion

Here we examined the potential correlation between the spatial variability of key ecological parameters across two big sagebrush hybrid zones, as well as the enhanced genetic variation conferred by hybridization. Variability in parental and hybrid plant responses (in terms of secondary chemicals, leaf elemental composition and biological absorption coefficients) to these ecological gradients were also examined in reciprocal transplant gardens across one hybrid zone. The results, while complex, nonetheless demonstrate several important points. First, the hybrid zone occurs at an ecotone. Prior analysis of the soils demonstrated that soil chemistry changes abruptly across the hybrid zone and becomes spatially more variable, particularly in the proportions of elements, within the hybrid zone. The vegetation goes from a floristically poor community in the basin zone to a very diverse community in the mountain zone. While the amount of ground cover is quite variable in the basin community, species composition is remarkably uniform. The reverse is true in the mountain zone. Species composition changes markedly from quadrat to quadrat, but the amount of plant cover is relatively uniform. The product of these two measures shows that the hybrid zone is intermediate for both trends and is more uniform in both the amount of cover

and species composition than either parental site. The insects found on sagebrush plants follow the same basic trends as the vegetation. The numbers of insects feeding on plants in the basin garden varied greatly among the plants, but the species composition of these insects was quite uniform. In the mountain garden (where there are considerably more species), the species composition of insects feeding on big sagebrush varied considerably from plant to plant, but insect density was quite uniform. The hybrid zone was intermediate just as it was with the vegetation. Thus it appears that the hybrid zone is found in a zone of sharp ecological transition.

The second major trend involves the reciprocal transplant gardens. Both insect and leaf chemistry data show variation among plants from the same source population to be greater for nonnative plants than those site-indigenous plants. This trend suggests that nonnative plants are more stressed than those indigenous to a particular site. This idea is not new; organisms under stress are known to display greater genetic variation (see Galaud and others 1993 for an excellent example). Similarly, insects are well known to prefer plants under stress (Whitham and others 1994; White 1976; Waring and Cobb 1992; Paige and Capman 1993). These results are, therefore, easy to understand in light of well-established patterns.

The third trend is that in the transplant gardens, overall, hybrids typically display greater plant-to-plant variation primarily in their biological absorption coefficients, but also in leaf chemistry. The source population term in the ANOVA model reflects at least a partial genetic contribution. Our findings that hybrids display greater variability is not surprising. Hybridization is well known to lead to increased phenotypic variability. This also corresponds well with our earlier results showing enhanced spatial variation in the proportions of elements in the soils (Wang and others 1998).

We have repeatedly shown that structuring of the big sagebrush hybrid zone is due to plant-by-soil interactions. Microbes are well known to mediate this type of interaction. A separate study (Miglia and others, in preparation) shows that the microbial community varies across the hybrid zone, and that growth of big sagebrush is contingent upon both the source population from which the plants originated and the microbial composition of the soils in which the plants were raised. This may partially explain the boundaries of the hybrid zone. Within each zone, indigenous plants should be under directional selection, thereby resulting in their adaptation to the indigenous microbial community. If this is true, then hybridization appears to provide the genetic variation needed to adapt to the more variable and unique edaphic properties (both biological and chemical) of the hybrid zone.

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