

Importance of Genotype, Soil Type, and Location on the Performance of Parental and Hybrid Big Sagebrush Reciprocal Transplants in the Gardens of Salt Creek Canyon

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Abstract: The majority of flowering plant species are descendent from hybridization events; therefore, understanding hybridization in nature is essential to understanding plant speciation. Hybrid zones, common and often stable, provide one source of hybridization. Stable hybrid zones are particularly important in evolutionary theory because they violate adaptive speciation theory and call into question the universality of reproductive isolation in speciation. Under this model, hybrids are assumed to be unfit regardless of environment, due to endogenous selection, thereby contributing to reproductive isolation. However, a number of stable hybrid zones show hybrids to be most fit within the hybrid zone due to ecological selection. Regardless of the type of selection occurring, stability of the hybrid zone results from a balance between gene flow and selection. What is not known is how hybridization allows hybrids to become adapted to the habitat of the hybrid zone. An understanding of the interactions between novel hybrid plant genotypes and their ecological habitats is important to understanding plant speciation. Results from a reciprocal transplant experiment involving the big sagebrush hybrid zone (*Artemisia tridentata* ssp. *tridentata* x *A. t.* ssp. *vaseyana*) in Salt Creek Canyon, UT, show that the parental and hybrid genotypes are not adapted to either the soils or location. Rather, it appears that the microorganisms in the soils are adapted to their location. It is possible that the plants are adapted to the microorganisms in their native soils. Our data also do not support the common assumption of hybrid unfitness.

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Introduction

Hybridization plays a key role in adaptive speciation theory (Dobzhansky 1940; Grant 1963; Mayr 1942; Stebbins 1950) because it is necessary for reinforcement of premating isolating barriers. Accordingly, the parental taxa are believed to diverge genetically due to some period of isolation, and subsequently come into contact again forming hybrids. If these hybrids are unfit they will be selected against, and genes that cause the parental species not to mate with each other will spread, generating or reinforcing premating isolating barriers, with the hybrids and hybridization eliminated over time. However, if hybrids are more fit than the parental taxa, then introgression will occur with the replacement of the parental taxa by introgressed populations. Either way the hybrid zone should be ephemeral. Stable hybrid zones violate adaptive speciation theory because hybrids can persist indefinitely (for example, the cottonwood hybrid zone studied by Eckenwalder [1984] is believed to be 2 million years old).

Three models (reviewed by Arnold 1997) seek to explain stable hybrid zones, with each postulating that selection balances gene flow. The models differ in the nature of that selection and the importance of the environment. Stable plant hybrid zones are particularly useful for studying these models because plants can be easily used in reciprocal transplant experiments (Emms and Arnold 1997; Wang and others 1997) and are often well adapted to local environmental conditions (reviewed in Linhart and Grant 1997), which is a key feature in adaptive speciation.

The *Dynamic Equilibrium Model* (Barton 1979a,b; Barton and Hewitt 1985, 1989; Hewitt 1988) posits that endogenous selection against hybrids balances gene flow into the hybrid zone, thereby accounting for hybrid zone stability. It is predicted that the hybrid zone will become trapped in areas of low population density, fixing it in space, but otherwise the model is environmentally neutral. Data from the big sagebrush hybrid zone (the subject of this report) does not support this model for two main reasons: big sagebrush

hybrids are more fit than the parental taxa within the boundaries of the hybrid zone, but less fit outside it (Wang and others 1997), and the hybrid zone does not occur in a population density trough (Freeman and others 1999a,b).

The *Mosaic Hybrid Zone Model* (Britch and others 2001; Harrison 1990; Harrison and Rand 1989; Howard and others 1993; Rand and Harrison 1989; Rieseberg and others 1998; Ross and Harrison 2002) also posits endogenous selection against hybrids, but assumes that the hybrid zone is a mosaic of parental habitats. Exogenous selection acts against the nonindigenous parental genotype, and while hybrids are always produced, their formation is balanced by endogenous selection against them. Again, data from the parental and hybrid big sagebrush at Salt Creek Canyon do not support this model because hybrids are the most fit genotype within the hybrid zone (that is, there is no endogenous selection against hybrids in the hybrid zone) and the hybrid zone is not a patchwork of the two parental habitat types (Freeman and others 1999a; Wang and others 1997, 1998).

The *Bounded Hybrid Superiority Model* (Moore 1977) assumes hybrid superiority in the hybrid zone, with selection against nonindigenous genotypes in both the parental and hybrid zone habitats. Hybrids are thus believed to be adapted within, but not outside, the hybrid zone, with the parental genotypes likewise superiorly adapted to their indigenous habitats. Prior results of our reciprocal transplant experiments are entirely consistent with this model (Freeman and others 1999a; Wang and others 1997, 1998, 1999). Implicit in this theory is that the parental and hybrid habitats differ from one another, as do the niches of the parental taxa and their hybrids. Wang and others (1998, 1999) found such niche separation when they analyzed the elemental composition of soils and leaves from plants in the reciprocal transplant gardens at Salt Creek Canyon. For example, basin habitat soils are deeper, and have a higher pH and lower concentrations of K, Mg, and Ba than soils from the mountain habitat. The soils in the hybrid zone have some elements in greater (Ca, K, Na) or lesser (Cu) concentrations than the soils of either parental habitat; therefore, they cannot be simply considered intermediate between the parental populations (Wang and others 1998). Similarly, the concentration of B in the leaves of basin parental plants was three times higher in the basin garden than in either the middle hybrid or mountain gardens, while the concentration of B in leaves of middle hybrid plants was nearly three times greater in the middle hybrid zone garden than in either the basin or mountain gardens. Mountain plants exhibited equal concentrations of B in their leaves in the two parental gardens, but markedly lower concentrations in the middle hybrid zone garden, and the concentration of B in their leaves was markedly lower overall compared to the other genotypes. In conclusion, the genotype by environment interactions for leaf elemental concentrations of plants all grown in the same three gardens strongly indicated niche separation.

Whittam (1989) proposed that herbivorous insects are more abundant in plant hybrid zones because hybridization disrupts defensive coadapted gene complexes, rendering hybrids more palatable than parental populations. We examined phytophagous insects in the Salt Creek reciprocal transplant gardens (Graham and others 2001a,b). The hybrid

zone and each parental habitat have unique insect communities, but the hybrids did not suffer higher insect densities. This again illustrates the different niches occupied by the different genotypes.

Plant community structure was not examined across the hybrid zone at Salt Creek Canyon because the area was reseeded; consequently, we examined the plant communities in a big sagebrush hybrid zone at Clear Creek Canyon in South Central Utah. We found that less than one-third of the species occur in both parental habitats; one-fourth of the species are unique to the basin habitat, and over half are unique to the mountain habitat. Fifteen species occur only within the hybrid zone (Freeman and others 1999a).

Together our prior data show that (1) basin and mountain big sagebrush and their hybrids are components of different biotic communities, (2) the hybrid zone occurs at an ecotone, and (3) hybrids are not universally unfit as the Dynamic Equilibrium and Mosaic Hybrid Zone models predict. Instead, genotype by environment interactions appear to be stabilizing the big sagebrush hybrid zone, in keeping with the predictions of the Bounded Hybrid Superiority model.

Methods

Our previous reciprocal transplant experiments involved growing parental and hybrid seedlings in the basin, mountain, and middle hybrid zone habitats. Because the taxa are parapatrically distributed along an elevational gradient, these earlier transplant experiments confounded both location and soils; consequently, we were unable to sort out the nature of the adaptation of the parental taxa and hybrids to their respective indigenous habitats. This confounding is especially true between the soils and temperature. Here, we report on a reciprocal transplant experiment in which both the soils and big sagebrush plants were transplanted into the gardens at Salt Creek Canyon.

Big Sagebrush

The big sagebrush (*Artemisia tridentata*) complex is a group of long-lived perennial, evergreen shrubs that dominates the landscape in the Western United States, providing forage for livestock and wildlife (Beetle 1960; McArthur 1994; Trimble 1989; Wambolt 1996; Welch and McArthur 1986). The species is composed of five subspecies: *A. t. ssp. tridentata* (basin big sagebrush), *A. t. ssp. vaseyana* (mountain big sagebrush), *A. t. ssp. wyomingensis* (Wyoming big sagebrush), *A. t. ssp. spiciformis* (snowbank big sagebrush), and *A. t. ssp. xericensis* (xeric big sagebrush). We examined one hybrid zone between basin and mountain big sagebrush. These subspecies differ genetically, morphologically, and ecologically from each other (table 1) and are sympatrically or parapatrically distributed, forming narrow hybrid zones along the sides of mountains or other points of contact.

Study Site

The study site is located in Salt Creek Canyon, near Nephi, in Juab County, UT, where basin and mountain big sagebrush are parapatrically distributed, with the basin subspecies occurring below 1,790 m in elevation and the

Table 1—Some characteristics that differ between basin and mountain big sagebrush.

Characteristic	Mountain	Basin	Reference
Habitat	Shallow, well-drained soils on foothills and mountains	Dry, deep, well-drained alluvial soils on plains, valleys, and foothills	McArthur 1994
Height	0.7 to 1.2 m	1.0 to 4.0 m	McArthur and Plummer 1978
Root system	Shallow	Deep	Welch and Jacobson 1988
Shoot morphology	<ul style="list-style-type: none"> • Spreading branches with an even-topped crown • Main stem is usually divided • Branches are layered 	<ul style="list-style-type: none"> • Erect, heavily branched shrub with an uneven-topped crown • Main stem is undivided (trunk-like) • Branches are not layered 	McArthur and others 1979
Leaf morphology	Broadly cuneate	Narrowly lanceolate	Beetle and Young 1965
Inflorescence	Spikate with many heads	Paniculate with few heads	Beetle and Young 1965
Palatability to mule deer	More palatable	Less palatable	Welch and McArthur 1986

mountain subspecies at elevations ranging from 1,850 m to timberline on neighboring Mt. Nebo (Graham and others 1995). The hybrid zone is a narrow band, approximately 380 m wide (per measurements by EDM and KJM in 2001), situated between the parental populations at elevations ranging from 1,790 to 1,830 m. Three fenced common gardens (8 by 15 m) were established across the hybrid zone in October 1994: one in each of the parental populations and one in the middle of the hybrid zone (Wang 1996).

Experimental Procedure

Battery operated HOBO™ Weather Station Data Loggers (Onset Computer Corp., Bourne, MA) were installed at each garden. This type of weather station can store up to 500,000 measurements, even if the batteries fail. Hourly temperatures were measured from September 12, 2000, until July 10, 2001. Hourly and daily average temperatures were analyzed using a mixed model ANOVA with site crossed with month and day nested within month. Daily, maximum, and minimum recorded temperatures were analyzed using a factorial design.

Putative reciprocal F₁, parental and indigenous hybrid seeds (B x M, M x B, B x B, M x M, and H x H, respectively, where B = basin big sagebrush, M = mountain big sagebrush, and H = hybrid between basin and mountain big sagebrush) were made in the field following the procedures of McArthur and others (1988). The first letter denotes the maternal parent and the second the paternal parent. While pollinations were highly controlled, some self-pollination may have occurred. In May 1999, seeds were germinated and subsequent seedlings raised in randomly arranged pots in the USDA Forest Service Shrub Sciences Laboratory greenhouse in Provo, UT. Seedlings were given equal amounts of water (table 2) when needed and pots rotated approximately every 6 weeks to balance any effects due to uneven greenhouse conditions. Greenhouse temperatures were controlled for favorable growth conditions (table 3). A 15:30:15 (available, water-soluble nitrogen:phosphate:potash) fertilizer solution was applied twice to the pots on January 25, 2000, and March 13, 2000. Five replicates of each genotype were planted in each of three soil types

(basin, mountain, and middle-hybrid zone) collected at sites immediately adjacent to the three common gardens. Three trenches (approximately 60 cm wide, 90 cm deep, and 12 m long) were excavated with a backhoe in each garden in May 2000, lined with 4 ml polyethylene sheeting,

Table 2—The watering schedule of seedlings during their stay in the greenhouse. The amounts listed are approximate averages.

Date	Amount	Date	Amount	Date	Amount
	<i>mL</i>		<i>mL</i>		<i>mL</i>
6/24/99	104.9	9/20/99	136.3	1/28/00	93.1
6/26/99	61.8	9/24/99	86.5	2/01/00	129.7
6/28/99	193.1	9/28/99	91	2/04/00	101.3
7/01/99	84.5	10/01/99	111.7	2/07/00	115.8
7/06/99	118.5	10/05/99	82.2	2/11/00	88.0
7/08/99	106.5	10/09/99	124.4	2/15/00	109.8
7/12/99	87.7	10/13/99	104.7	2/18/00	74.8
7/14/99	117.6	10/15/99	97.9	2/22/00	86.4
7/16/99	77.9	10/21/99	72.8	2/25/00	79.4
7/19/99	122.8	10/27/99	111.1	2/28/00	87.5
7/21/99	53.8	11/01/99	90.0	3/03/00	106.7
7/23/99	120.9	11/04/99	111.4	3/06/00	93.7
7/26/99	94.7	11/08/99	98.8	3/10/00	117.2
7/28/99	118.8	11/12/99	100.0	3/13/00	157.4
7/30/99	83.6	11/16/99	136.5	3/17/00	160.7
8/01/99	115.3	11/22/99	85.5	3/20/00	164.2
8/04/99	102.4	11/27/99	160.7	3/24/00	137.5
8/07/99	74.2	12/01/99	78.4	3/27/00	152.9
8/09/99	128.7	12/06/99	125.1	3/31/00	166.1
8/12/99	123.4	12/13/99	87.5	4/03/00	137.9
8/14/99	99.8	12/16/99	186.6	4/06/00	160.5
8/17/99	102.6	12/20/99	116.0	4/09/00	135.5
8/20/99	121.0	12/23/99	70.8	4/12/00	187.9
8/23/99	101.0	12/26/99	60.1	4/14/00	207.8
8/26/99	70.6	12/29/99	80.6	4/17/00	187.6
8/29/99	57.8	1/02/00	108.6	4/19/00	190.8
9/01/99	103.9	1/06/00	75.3	4/21/00	69.0
9/07/99	120.1	1/10/00	66.8	4/24/00	170.0
9/09/99	100.5	1/14/00	115.7	4/28/00	174.0
9/11/99	96.4	1/17/00	75.3	5/01/00	125.0
9/14/99	114	1/21/00	87.3		
9/17/99	150.1	1/25/00	86.0		

Table 3—The average minimum and maximum temperatures in the greenhouse during the first year of seedling growth.

Month/year	Minimum temperature	Maximum temperature	N
	-----°C-----		
6/99	13	41	21
7/99	15	40	31
8/99	16	38	31
9/99	9	35	30
10/99	8	39	31
11/99	8	35	30
12/99	9	34	31
1/00	9	31	31
2/00	9	34	29
3/00	10	37	31
4/00	10	39	30
5/00	11	36	8

and then filled with one of the same three soil types used in the greenhouse (that is, each of the three soil types was represented in each garden, including the indigenous soil type for each garden). One-year-old seedlings were then planted at random in the soil-filled trenches, with the choice of trench corresponding to the soil type to which a seedling was exposed during its stay in the greenhouse. There were 25 transplants per trench, giving a total of 75 transplants per garden. Each plant was marked with a labeled rebar. Plants were watered in the gardens weekly until watering was tapered to once every other week in mid-August 2000 and then stopped completely in mid-September 2000.

Data Collection and Statistical Analyses

Measurements were taken in August 2001 and August 2002 for the following growth and reproductive parameters: crown diameters 1 and 2 (crown 1 = greatest diameter of plant; crown 2 = diameter directly perpendicular to crown 1), tallest vegetative branch, tallest branch (tallest vegetative branch plus tallest inflorescence branch, when present), and length of three representative inflorescences

All temperature and morphological data were analyzed using the SPSS version 10.0 statistical software (SPSS Inc. 2001). All morphological data were analyzed using a MANOVA (SPSS Inc. 2001). Cases involving equal variances were followed by Bonferroni *post hoc* tests (SPSS). Data violating the assumption of equal variances were square-root transformed. In those cases where data transformation did not yield equal variances, Dunnett's T3 *post hoc* tests were performed (SPSS Inc. 2001).

Results

Temperature

The average daily minimum temperature differed significantly among the sites ($F_{2,873} = 19.20$, $P < 0.001$), with the basin garden site having the lowest average daily minimum temperature and the mountain garden site having higher

daily minimum temperatures than either the basin or middle hybrid zone garden sites (table 4). The average daily and maximum temperatures did not differ significantly among the gardens; however, the middle hybrid zone garden site had both the lowest average daily temperature and highest average maximum temperature (table 4).

Height

We measured height two ways. First, we measured the height of the tallest vegetative branch and second, the height of the tallest branch that included an inflorescence. Both measures of height differed significantly among the gardens ($F_{2,152} = 8.117$, and 2.54 , $P < 0.001$ and 0.08 , respectively). Plants in the middle hybrid zone garden were significantly taller than those in the parental gardens; the average height of plants in the parental gardens did not differ from each other (table 5). Vegetative height also differed significantly among the genotypes ($F_{2,152} = 5.39$, $P < 0.001$). Both types of F_1 hybrids were significantly shorter than either the basin or indigenous hybrid plants. The F_1 plants did not differ in size from the mountain plants nor did mountain plants differ from either the basin or indigenous hybrid plants.

Vegetative height was independent of soil type; however, when the inflorescences were included, the middle hybrid zone soils produced significantly shorter plants than the other two soil types, which did not differ from each other. There was a highly significant garden by soil type interaction for both the vegetative and vegetative plus inflorescence measures of height ($F_{4,152} = 3.035$, and 7.574 , respectively; $P < 0.02$ and 0.001 , respectively). The trend was most dramatic for the inflorescence measure. In the basin garden, plants grew best in the basin soils. However, in the middle hybrid zone garden, middle hybrid zone soils yielded the greatest height. There was no trend observed for this measure in the mountain garden (figs. 1b and 1c).

Crown Diameter

Average crown diameter differed significantly among the genotypes ($F_{4,152} = 4.23$, $P < 0.003$), but not among the gardens or soil types (table 6). Basin plants produced significantly smaller crown diameters than the other four genotypes, which did not differ among themselves. The garden by soil interaction was also significant ($F_{4,152} = 3.45$, $P < 0.01$) (fig. 1d). Indigenous hybrids produced their greatest crown diameter in the middle hybrid zone garden in the middle hybrid zone soils, whereas both of the parental genotypes

Table 4—Temperature profiles in each of the three gardens^a.

Site	Average daily temperature	Average daily minimum temperature	Average Daily maximum temperature
Basin	8.10a	-2.01a	18.66a
Hybrid	7.78a	-1.64a	19.68a
Mountain	8.14a	-0.10b	18.79a

^aDifferent letters in columns indicate significant ($P < 0.05$) differences among values.

Table 5—Averages for vegetative height, vegetative plus inflorescence height, average inflorescence length and crown diameter for plants in each of the three gardens^a.

Garden	Vegetative height	Height including inflorescence	Average inflorescence length	Average crown diameter
----- <i>cm</i> -----				
Basin	45.50a	48.62a	16.35a	43.56a
Hybrid	51.17b	54.22b	19.75b	48.37a
Mountain	43.09a	44.94a	16.58a	43.99a

^aDifferent letters in columns indicate significant ($P < 0.05$) differences among values.

Table 6—Averages for vegetative height, vegetative plus inflorescence height, average inflorescence length and crown diameter for each of the five genotypes^a.

Genotype	Vegetative height	Height including inflorescence	Average inflorescence length	Average crown diameter
----- <i>cm</i> -----				
B x B	51.02a	46.37a	15.42a	38.54a
B x M	40.38b	41.41a	15.43a	48.02b
M x B	43.50b	52.80a	19.49a	45.39b
M x M	50.42a	54.02a	19.46a	46.68b
H x H	45.81ab	49.79a	17.52a	49.04b

^aDifferent letters in columns indicate significant ($P < 0.05$) differences among values.

produced their greatest crown diameters in the basin garden in the basin soils.

Inflorescence Length

The average inflorescence length differed significantly among the gardens ($F_{2,152} = 2.87$, $P < 0.06$) and soils ($F_{2,152} = 5.74$, $P < 0.005$), but not among the genotypes. Plants in the middle hybrid zone garden produced significantly longer inflorescences than in the other two gardens, which did not differ from each other. Plants in the basin soils produced longer inflorescences than did plants in the middle hybrid zone soils. Inflorescence length of plants in the mountain soils was intermediate between those in the middle hybrid zone and basin soils and did not differ significantly from either. There was a highly significant garden by soil interaction ($F_{4,152} = 9.85$, $P < 0.001$). Plants in the middle hybrid zone soils performed very poorly in the basin garden, while in the middle hybrid zone garden, plants in the middle hybrid zone soils performed better than in the other two soil types (fig. 1a).

Discussion

Our findings indicate that the minimum temperature differed greatly across the hybrid zone. This finding coupled with those examining soils (Wang and others 1998), elemental leaf concentrations (Wang and others 1999), and the insect (Graham and others 2001a,b) and plant communities (Freeman and others 1999b) strongly indicate that the habitats occupied by the parental taxa and their hybrids are distinct from one another. Thus, the big sagebrush hybrid zone occurs at an ecotone. Our results also confirm earlier

studies showing that the different subspecies of big sagebrush exhibit different morphologies and that these differences are preserved in common gardens—indicating a genetic basis for both the growth habits and niche separation (McArthur 1994; McArthur and others 1979; McArthur and Welch 1982). However, our most important result from this study is somewhat disconcerting. Earlier work (Wang and others 1997) had shown that basin and mountain big sagebrush are each adapted to their indigenous habitat and that indigenous hybrids were the most fit genotype within the hybrid zone. The transplant experiments involved in that study confounded the physical location with the soils. In the present study, we reciprocally transplanted both the soils and seedlings into the gardens to sort out these effects, if any. We anticipated that the seedlings might be adapted to their indigenous soils and perhaps their indigenous physical location, as well. This is not what we observed. Neither the genotype-by-garden nor garden-by-soil interactions were significant for any variable. However, the garden-by-soil interaction was significant for every variable, which was indicative of adaptation in two cases: basin soils in the basin garden and middle hybrid zone soils in the middle hybrid zone garden. This leads us to conclude that the indigenous soils are adapted at each of these locations, implying that it is the soil microorganisms that have become adapted to a particular location and not the plants themselves. The results of this study coupled with our earlier results (Wang and others 1997) imply that the different genotypes must be adapted to the indigenous microorganisms and that these microorganisms are adapted to the soils and physical location in the garden of their indigenous habitat. We have yet to determine whether or not this is case, and also if the microorganisms in the middle of the hybrid zone are distinct from those in either parental habitat. If our conclusions are

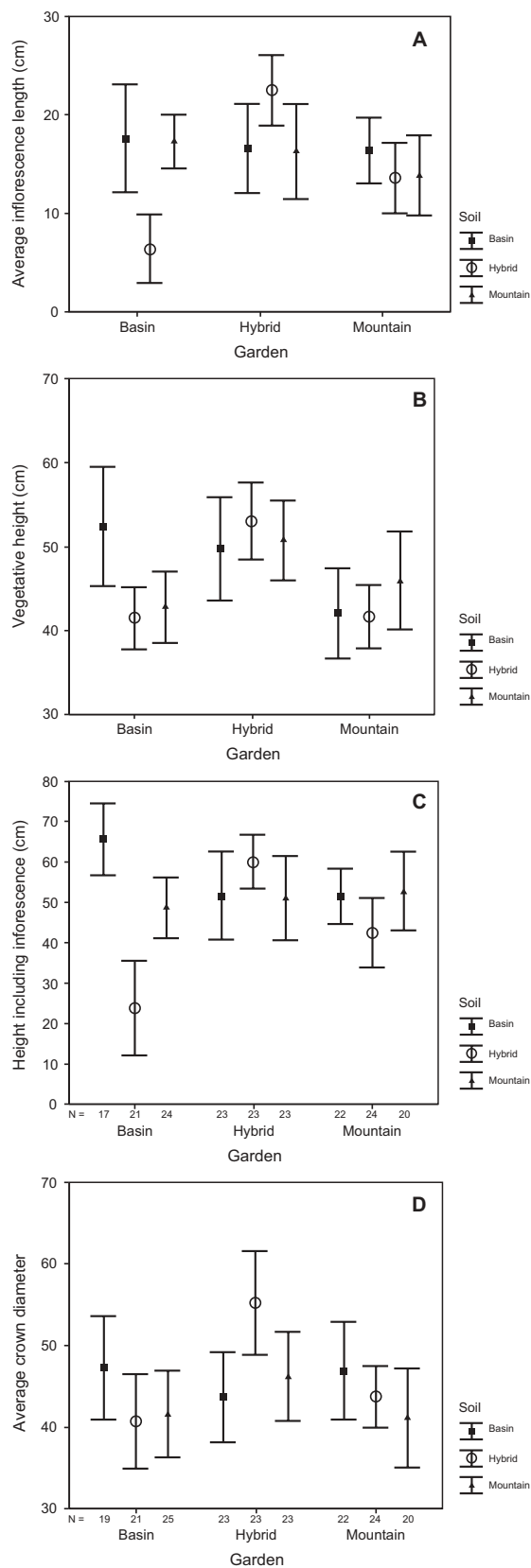


Figure 1—Mean (A) average inflorescence length of plants, (B) vegetative height, (C) vegetative height including inflorescence, and (D) average crown diameter in each of the three soils in each of the three gardens.

correct, then hybrid zone theory needs to be expanded to include symbiotic interactions as well as the physical and chemical aspects of the environment.

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