

Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). VI. Respiration and water potential

E. Durant McArthur, D. Carl Freeman, John H. Graham, Han Wang, Stewart C. Sanderson, Thomas A. Monaco, and Bruce N. Smith

Abstract: Respiration and stem water potential (ψ) were examined in parental and hybrid big sagebrush (*Artemisia tridentata* Nutt. ssp. *tridentata* and *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) grown in common gardens within each parental zone and in the hybrid zone. Plants were sampled in July, August, and September, i.e., immediately before, during, and after flowering. The habitats differed from one another, and there were significant garden by date interactions. The source populations also differed significantly from one another. There were no significant garden by source interactions. Hybrid plants had intermediate respiration rates and did not suffer greater water stress than parental plants. Hybrid plants showed no apparent decrease in adaptation in the important physiological traits respiration and water stress in the hybrid zone.

Key words: *Artemisia*, hybrid zones, respiration, water potential.

Résumé : Les auteurs ont examiné la respiration et le potentiel hydrique de la tige (ψ) chez des plantes parentes et hybrides de la grande arthémise (*Artemisia tridentata* Nutt. ssp. *tridentata* et *Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) cultivées dans des jardins communs dans chacune des zones parentales et dans la zone d'hybridation. Ils ont échantillonné les plantes en juillet, août et septembre, i.e., immédiatement avant, durant et après la floraison. Les habitats diffèrent les uns des autres, et on a observé des différences significatives entre les jardins selon les dates. Les populations d'origine diffèrent également significativement les unes des autres. Il n'y a pas d'interaction significative entre jardins et origines. Les plants hybrides montrent des taux de respiration intermédiaires et ne souffrent pas plus fortement du stress hydrique que les plants parentes. Dans la zone d'hybridation, les plantes hybrides ne montrent pas de diminution apparente d'adaptation relativement à deux caractères physiologiques importants, soient la respiration et le stress hydrique.

Mots clés : *Artemisia*, zones d'hybridation, respiration, potentiel hydrique.

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Introduction

Stable hybrid zones occur when both allopatric and sympatric populations of parental taxa persist despite the exchange of genetic material within hybrid zones. The factors responsible for stabilizing hybrid zones have been the subject of numerous investigations (Barton 1979; Barton and Hewitt 1981, 1985, 1989; Harrison 1986, 1990; Bert and Harrison 1988; Harrison and Rand 1989; Bennett and Grace 1990; Bert and Arnold 1995). Two basic models have been proposed to account for the stability of hybrid zones. Both models assume that gene flow is balanced by selection, but they differ in their assumptions. The ecologically neutral dynamic-equilibrium model assumes that hybrids are universally less fit and that this drop in fitness is due to the disruption of coadapted gene complexes

(Barton and Hewitt 1985). In contrast, the ecologically dependent bounded hybrid-superiority model (Endler 1977; Moore 1977) assumes that selection favors each hybrid and parental taxon within its native (indigenous) habitat, i.e., that selection is the result of genotype by environment interactions. Hybrids are assumed to be more fit than either parental taxon within the hybrid zone but less fit outside the hybrid zone. Central to the study of any of these phenomena related to hybrid zones is the assessment of the relative fitness of the parental taxa and their hybrids. This assessment is best done using field reciprocal transplant experiments; such experiments avoid the confounding of genotype and environment inherent in purely descriptive studies.

Relative fitness is a complex measure of how well a genotype is adapted to a particular environment and thus is dependent

E.D. McArthur¹ and S.C. Sanderson. Shrub Sciences Laboratory, Rocky Mountain Research Station, USDA Forest Service, 735 North 500 East, Provo, UT 84606, U.S.A.

D.C. Freeman and H. Wang.² Department of Biological Sciences, Wayne State University, Detroit, MI 48202, U.S.A.

J.H. Graham. Department of Biology, Berry College, Mount Berry, GA 30149, U.S.A.

T.A. Monaco³ and B.N. Smith. Department of Botany and Range Science, Brigham Young University, Provo, UT 84602, U.S.A.

¹ Author to whom all correspondence should be addressed.

² Present address: Institute of Molecular Medicine and Genetics, Medical College of Georgia, Augusta, GA 30912, U.S.A.

³ Present address: Department of Rangeland Ecology and Management, Texas A & M University, College Station, TX 77843, U.S.A.

upon a variety of life-history features and physiological processes. Given the importance of assessing relative fitness, the paucity of both reciprocal transplant experiments and physiological studies in hybrid zone research is unfortunate. Most hybrid zone research has been conducted on mobile animals, making transplant experiments difficult. Botanists have a long tradition of studying hybridization (e.g., Anderson and Hubricht 1938; Baker 1951; Stebbins 1959; Alston and Turner 1963; Levin 1963; McArthur et al. 1988; Potts and Reid 1988; Arnold 1992), and conducting reciprocal transplant experiments (Clausen et al. 1940, 1948), but the two approaches have rarely been combined (Potts 1985). In instances when those approaches have been combined, the performance of the parents in the hybrid zone and of the hybrids in the parental zone has rarely been measured, which precluded a complete assessment of relative fitness (but see Levin and Schmidt 1985; Schmidt and Levin 1985; Young 1996; Wang et al. 1997). Plant hybridization is often described as occurring within "hybrid swarms" (Harrison 1993). Usually, it is not known whether or not hybrid swarms occur as congruent clines or mosaics, i.e., if they are structured. The term swarm itself implies a lack of structure, though in reality it may be difficult to differentiate between hybrid swarms and mosaic hybrid zones. Nevertheless, it is the stability of the spatial structure of hybrid zones that makes them so important and intriguing. It is this stability that demands an explanation.

Here, we report the results of respiration and water potential investigations of reciprocal transplant experiments across a narrow hybrid zone between basin (*Artemisia tridentata* Nutt. ssp. *tridentata*) and mountain (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) big sagebrush. Previously, we have shown that these subspecies differ in growth (McArthur and Welch 1982; McArthur et al. 1988), morphology (Freeman et al. 1991), flower and seed production (Graham et al. 1995; Wang et al. 1997), genetics (McArthur et al. 1998), biochemistry (McArthur et al. 1988; Weber et al. 1994; Byrd 1992; Byrd et al. in review), and associated insects (Graham et al. 1995; Messina et al. 1996). For each of these traits the clines are congruent, indicative of a stable hybrid zone. The habitats of parental and hybrid plants differ in mineral element concentration, soil depth, soil pH, and plant community composition (McArthur et al. 1988; Graham et al. 1995; Wang 1996; Wang et al. 1998). Concentration of mineral elements and mineral element biological absorption coefficients (= differential absorption in plants with respect to availability in the soil) differ among habitats within the hybrid zone and among the parental and hybrid plants, and demonstrate significant genotype by environment interactions (Wang et al. in review). Furthermore, the results of reciprocal transplant studies show significant genotype by environment interactions for seed germination, survivorship, growth, and a variety of reproductive parameters, with hybrids exhibiting higher fitness than either parent in the hybrid zone and each parent being most fit in its indigenous site (Graham et al. 1995; Wang 1996; Wang et al. 1997).

Physiological measurements are important in our studies of big sagebrush hybrid zones to complement earlier studies on plant morphology, selection gradients, fitness, developmental instability, reciprocal transplantation, soil properties, and chemistry (Freeman et al. 1991, 1995; Byrd 1992; Graham et al. 1995, Wang 1996; Wang et al. 1997, 1998). Photosynthesis is the key physiological process. It is the conversion of

light energy, water, and carbon dioxide into organic matter. All biological growth is dependent on this process. However, during the past 20 years, many investigators have tried without success to establish correlations between rates of photosynthesis and growth rates (Nelson 1988). Much better results have been obtained by looking at dark respiration as a predictor of growth (Hay and Walker 1989). Earlier work with big sagebrush supported this view (Frank et al. 1986). Both respiration rate and stem water potential can be made quickly at field locations (Waring and Cleary 1967; Field et al. 1989). The information obtained from those physiological parameters allows accurate predictions of growth rates of plants from parent and hybrid populations in response to environmental stresses, in this case temperature and water availability.

Materials and methods

Study site

The study site is located in the Salt Creek drainage in Juab County, Utah, ranging in elevation from 1780 m at the basin big sagebrush site to 1870 m at the mountain big sagebrush site over a 1.1 km linear distance extending from the Salt Creek floodplain up Salt Cave Hollow in a westerly direction (see Freeman et al. 1991; Graham et al. 1995; and Wang 1996 for a more complete description). The soils range from well-drained dark brown loam at the basin big sagebrush site through stony loam in the hybridization area to gravelly loam at the mountain big sagebrush site (Trickler and Hall 1984) and vary by site in pH, thickness, and mineral concentrations (Wang 1996). Precipitation is about 560 mm annually with about 65% of that coming from October to April, much of it as snow (Richardson et al. 1981; Ashcroft et al. 1992). The water year of this study (October 1994 – September 1995) was wetter than the long-term average, but average daily temperatures were normal. The closest weather stations, Nephi, 1347 m elevation and 10 km west (252°), received 581 mm (157% of normal) and Fairview, 1817 m in elevation and 27 km east (115°), received 549 mm (159% of normal) precipitation (Ashcroft et al. 1992; National Oceanic and Atmospheric Administration 1994, 1995). However, the summer period (July–September) was dry with normal temperatures; precipitation was 86% (62 mm) of normal at Nephi and 91% (75 mm) of normal at Fairview; area daily average temperatures were within 0.5°C of long-term averages (Ashcroft et al. 1992; National Oceanic and Atmospheric Administration 1994, 1995).

Our studies at the Salt Creek hybrid zone have included analyses of plants and their habitats in five sites within the zone that we have labeled basin population (1780 m, "pure" basin big sagebrush population), near-basin population (1790 m, much like basin big sagebrush but with influence from mountain big sagebrush plants, 260 m upslope from basin population), hybrid population (1800 m, includes substantive elements of both basin and mountain big sagebrush plants, 200 m upslope from near-basin population), near-mountain population (1820 m, much like mountain big sagebrush but with influence from basin big sagebrush plants, 360 m upslope from hybrid population), and mountain population (1870 m, "pure" mountain big sagebrush, 240 m upslope from near-mountain population) (Freeman et al. 1991, 1995; Byrd 1992; Graham et al. 1995; Wang 1996; Wang et al. 1997, 1998, in review; Byrd et al. in review). In May of 1993 we established three reciprocal transplant gardens (ca. 8 × 15 m): within the basin population (basin garden), within the hybrid population (hybrid garden), and within the mountain population (mountain garden). The stock placed in the transplant gardens was 1-year-old plants grown from seed in a greenhouse including three half-sib families of four plants each from each of the basin, near-basin, hybrid, near-mountain, and mountain populations. The genetic makeup of these families is not known except the maternal (seed-bearing, open-

Table 1. Analysis of variance of respiration data for the effects of garden, source population, and date.

Source of variation	df	MS	F
Among subjects			
Garden	2	249 817.1	23.9***
Source	4	44 355.2	4.3**
Garden × source	8	29 240.0	1.4ns
Plant (garden × source)	15	20 414.0	2.0*
Replication (plant (garden × source))	146	10 419.7	
Within subjects			
Date	2	138 220 174.0	1836.6***
Garden × date	4	67 318.4	8.9***
Source × date	8	10 747.2	1.4ns
Garden × source × date	16	22 568.5	1.1ns
Plant (garden × source × date)	30	20 145.6	2.7***
Replication (plant (garden × source × date))	292	7 524.9	

Note: Repeated measures are on date. For the within-subject tests the significance of *F* was determined for adjusted degrees of freedom, which equal $df \times \text{Huynh-Feldt } \epsilon$ (0.73544). *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant.

pollinated) parents conformed to basin, near-basin, hybrid, near-mountain, and mountain phenotypes on morphological and chemical (coumarin and terpenoid) criteria (McArthur et al. 1988; Freeman et al. 1991). The gardens were fenced, for protection, with 2.5-m high fences in October 1994. Gardens were established on sites that appeared to be homogeneous.

Respiration

Respiration (CO_2 evolution in $\mu\text{g}\cdot\text{min}^{-1}\cdot\text{g}^{-1}$ dry weight) was measured with a LI-COR 6250 infrared gas analyzer (LI-COR Inc., Lincoln, Neb.). Leaf material was saved and oven-dried at 65°C for mass determination. Measurements were recorded for three successive 1-min intervals per sample. Respiration rates were measured on July 6, 1995, August 8, 1995, and September 28, 1995. Measurements were made at a central field location at the near-mountain population site for two samples from each of two plants from two of the three half-sib families from each garden. The same individual plants and sampling order was maintained over the three sampling dates. Order of sampling was determined by a random sequence from each garden, but gardens were sampled in an integrated way so that a plant from each of the basin garden, mountain garden, and hybrid garden was sampled before the garden sequence was repeated. It took about 7 h to complete the sampling each sampling day.

Water potential

Water potential (ψ) in MPa was sampled before sunrise (ψ_{predawn}), and at midday (ψ_{midday}) on July 6, 1995, August 8, 1995, and September 28, 1995 using a Scholander Pressure Bomb (PMS 1000, PMS Corp., Corvallis, Oreg.) at our central near-mountain population location. The same two samples from each of two plants from two of the three half-sib families from each garden that were used in the respiration portion of the study were also used for the water potential examination. Order of sampling was in the same random sequence described in the respiration study (see previous paragraph). Sample plants and sampling sequence were the same for ψ_{predawn} and ψ_{midday} samples and on all three sampling dates. Each data set took about 2.5 h to collect.

Data analysis

We used an analysis of variance that took into account garden (basin garden, hybrid garden, mountain garden), source population (basin population, near-basin population, hybrid population, near-mountain population, mountain population), and date, with repeated measures on date and time of day (Winer 1962). For the within-subjects tests, we adjusted the degrees of freedom by multiplying both the numerator and denominator degrees for freedom by the Huynh-Feldt ϵ

(Huynh and Feldt 1976). All analyses were done with SPSS's MANOVA procedure (Norusis 1994). We accepted significant differences at $P < 0.05$ and report the mean \pm SE, based on among plant variances.

Results

Respiration

There were significant differences in respiration rates among the three gardens (Table 1). Respiration rates (means for transplants from all sources) were highest in the hybrid garden ($347 \pm 49 \mu\text{g CO}_2\cdot\text{min}^{-1}\cdot\text{g}^{-1}$, $N = 30$) and lowest in the mountain garden ($273 \pm 39 \mu\text{g CO}_2\cdot\text{min}^{-1}\cdot\text{g}^{-1}$, $N = 30$); the respiration rate for the basin garden was intermediate ($312 \pm 18 \mu\text{g CO}_2\cdot\text{min}^{-1}\cdot\text{g}^{-1}$, $N = 30$). There were also significant differences in respiration rates among the source populations. The basin population and near-basin population had the highest respiration rates (basin population, $332 \pm 60 \mu\text{g CO}_2\cdot\text{min}^{-1}\cdot\text{g}^{-1}$, $N = 18$; near-basin population, $329 \pm 60 \mu\text{g CO}_2\cdot\text{min}^{-1}\cdot\text{g}^{-1}$, $N = 18$); the hybrid population and near-mountain population had intermediate rates (hybrid population, $303 \pm 57 \mu\text{g CO}_2\cdot\text{min}^{-1}\cdot\text{g}^{-1}$, $N = 18$; near-mountain population, $303 \pm 60 \mu\text{g CO}_2\cdot\text{min}^{-1}\cdot\text{g}^{-1}$, $N = 18$); and the mountain population had the lowest rate ($286 \pm 56 \mu\text{g CO}_2\cdot\text{min}^{-1}\cdot\text{g}^{-1}$, $N = 18$). The differences in respiration rates among the three dates were significantly different as well (Table 1). The respiration rate was highest in July, declined in August, and was lowest in September (Fig. 1). There was also a significant decline through the season in the gardens (Table 1, Fig. 1); the decline in respiration rate throughout the season was less pronounced in the mountain garden than in the basin garden and hybrid garden.

Water potential

There were significant differences in ψ among plants in the three gardens (Table 2). Plants in the hybrid garden were less water stressed (-1.84 ± 0.06 MPa, $N = 120$) than were plants in the mountain garden (-2.09 ± 0.07 MPa, $N = 120$) and basin garden (-2.16 ± 0.07 MPa, $N = 120$) (means for all sources, predawn and midday data combined). There were, however, significant garden by date, and garden by date by time interac-

Fig. 1. Effect of garden and date on the mean respiration rate. Each data point is based on $N = 10$. Standard errors are small and nonoverlapping (July range 28.18–31.07; August range 9.37–16.86; September range 7.94–10.20).

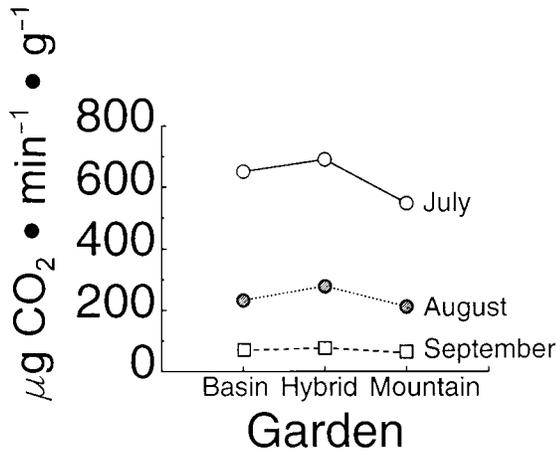
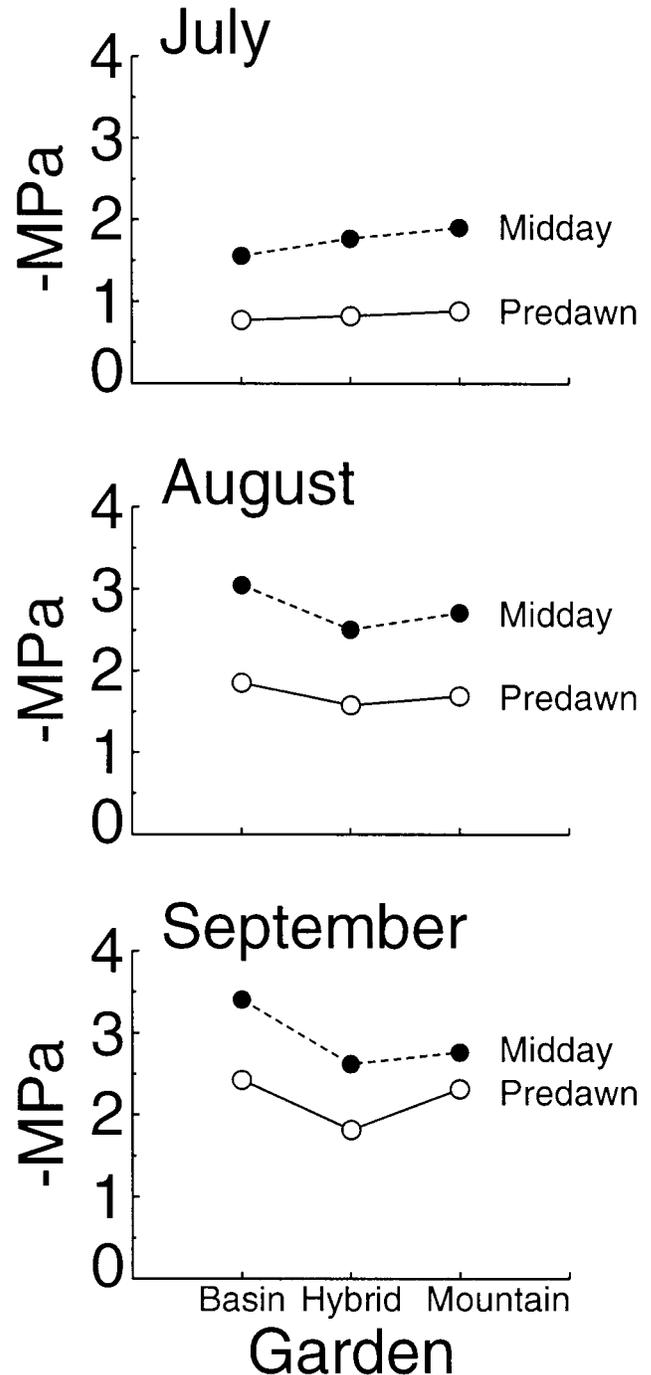


Table 2. Analysis of variance of water potential data for the effects of garden, source population, and date.

Source of variation	df	MS	F
Among subjects			
Garden	2	6.82	12.42**
Source	4	2.97	5.41**
Garden × source	8	0.83	1.51ns
Plant (garden × source)	15	0.55	1.21ns
Replicate (plant (garden × source))	90	0.46	
Within subjects			
Date	2	103.83	235.98***
Garden × date	4	4.00	9.10***
Source × date	8	0.40	0.92ns
Garden × source × date	16	0.33	0.74ns
Plant (garden × source × date)	30	0.44	2.12**
Replicate (plant (garden × source × date))	180	0.21	
Time	1	162.09	1157.79***
Garden × time	2	0.35	2.52ns
Source × time	4	0.16	1.12ns
Garden × source × time	8	0.15	1.05ns
Plant (garden × source × time)	15	0.14	3.00**
Replicate (plant (garden × source × date × time))	90	0.05	
Date × time	2	1.24	13.78***
Garden × date × time	4	0.86	9.63***
Source × date × time	8	0.15	1.66ns
Garden × source × date × time	16	0.07	0.80ns
Plant (garden × source × date × time)	30	0.09	1.50ns
Replicate (plant (garden × source × date × time))	180	0.06	

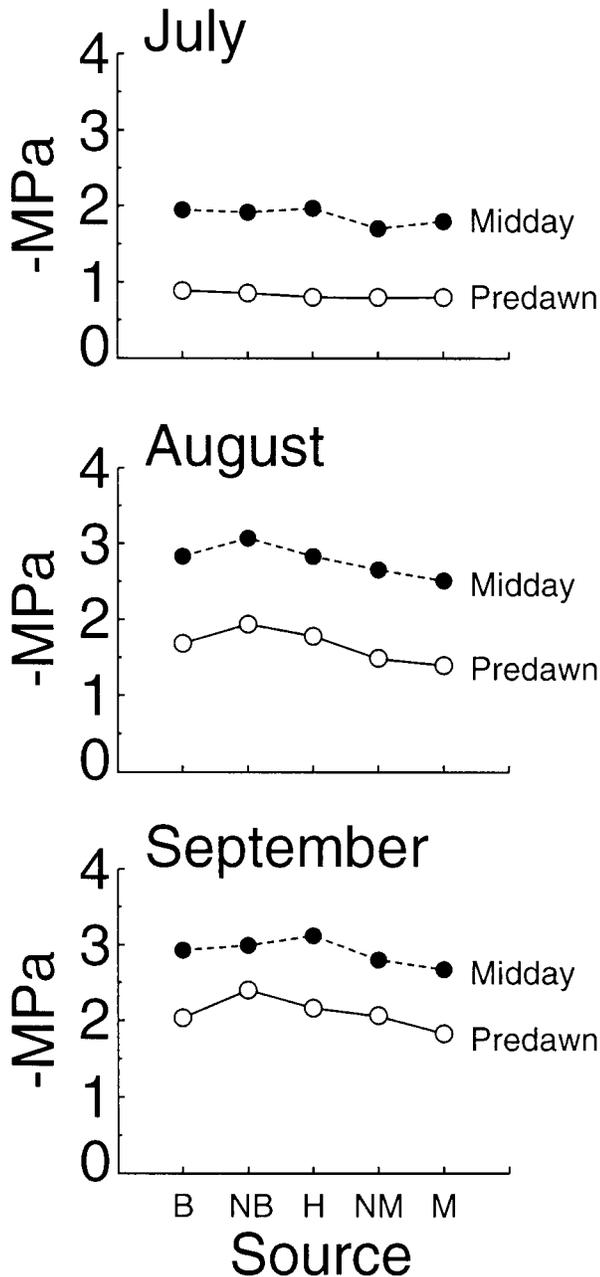
Note: Repeated measures are on date and time. For the within-subject tests the significance of F was determined for adjusted degrees of freedom, which equal $df \times \text{Huynh-Feldt } \epsilon$. The ϵ values were as follows: date, 0.9015; date × time, 0.9161; date × other variables, 0.6352; date × time with other variables, 1.0000. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. ns, not significant.

Fig. 2. Effect of garden, date, and time with respect to water potential. Each data point is based on $N = 20$. Standard errors are small and nonoverlapping (July range 0.030–0.095; August range 0.052–0.124; September range 0.036–0.191).



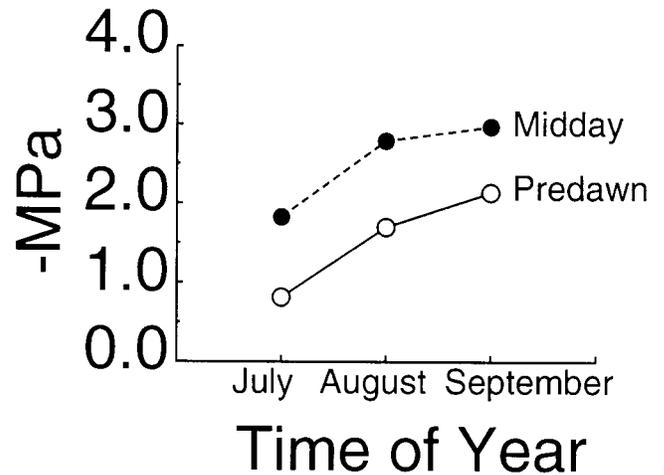
tions to complicate this relationship. These interactions are evident in Fig. 2. During July, ψ was nearly the same in all three gardens. But as the season progressed, water stress increased to a greater extent in the basin and mountain gardens than in the hybrid garden. In addition to differences among the gardens, there were also significant differences in stem water potential among the five source populations (Table 2). In general, mountain population (-1.85 ± 0.09 MPa, $N = 72$) and

Fig. 3. Effect of source population, date, and time with respect to water potential. B, basin population; NB, near-basin population; H, hybrid population; NM, near-mountain population; M, mountain population. Each data point is based on $N = 12$. Standard errors are small and nonoverlapping (July range 0.032–0.130; August range 0.064–0.200; September range 0.106–0.258).



near-mountain population (-1.93 ± 0.10 MPa, $N = 72$) plants were less stressed, regardless of garden, season, and time of day, while basin population (-2.06 ± 0.10 MPa, $N = 72$), near-basin population (-2.21 ± 0.11 MPa, $N = 72$), and hybrid population (-2.12 ± 0.11 MPa, $N = 72$) plants were more stressed (Fig. 3).

Fig. 4. Effect of date and time with respect to water potential. Each data point is based on $N = 60$. Standard errors are small and nonoverlapping (July range 0.023–0.046; August range 0.052–0.062; September range 0.086–0.094).



Date and time-of-day (within-subject effects) also had significant influences on ψ (Table 2). In general, plants increased in water stress from July through August to September. Moreover, water is moved more easily through the plants before dawn than during the middle of the day (Figs. 3 and 4). There was a significant interaction between day and time (Table 2, Fig. 4). Differences in stem water potential between predawn and midday were less in September than they had been in July or August. By September, predawn stem water potentials were more negative than midday potentials had been in July.

Discussion

Both the respiration rate and stem water potential data demonstrate that hybrid plants are different in these characteristics from parental plants. These differences were sometimes manifested among the gardens, among the source populations, or both and over time. Some interactions were significant. Differences between source populations could, perhaps, be attributed to rooting depth, stomatal conductance, and (or) hydraulic conductance differences. Differences in respiration may be related to growth rates and enzyme pools. The two parental subspecies differ in many morphological and physiological characteristics (see McArthur and Plummer 1978; Freeman et al. 1991; McArthur and Stevens 1998 for review and summary). Hybrid plants could combine these characteristics in many novel ways for habitat selected advantages. Even as the basin and mountain big sagebrush plants are different from one another and have variation within each parental class, the hybrid plant respiration and water potential data demonstrate that these plants behave as a class separate from the parentals, but like the parentals, they also have complex and variable expression of these physiological traits.

Hybrids are apparently as well adapted as parentals. They showed intermediate rates of respiration and were not under greater water stress than parentals. Respiration and water potential are important traits. Respiration, simply put, is the principal means by which plants are able to utilize stored energy

for growth, reproduction, defense, and other functions. Thus, the respiration patterns of the plants in this study bear importantly on their adaptation to the test and natural habitats in which they were examined over the growing season. Likewise, all else being equal, lower water potential means lower stomatal conductance and less potential for photosynthesis and nutrient uptake.

Differences between gardens could be due to ambient temperature and soil hydrology differences. Differences between dates could be in response to temporal temperature differences and soil drought. The time of study covered only one season. The season (July–September) was slightly drier (88%) than normal, although the water year (October–September) as a whole was wetter (158%); seasonal and water-year temperatures were approximately normal (Ashcroft et al. 1992; National Oceanic and Atmospheric Administration 1994, 1995). Additional seasons of data collection (B.N. Smith, unpublished data) might reveal genotype by environment interaction in physiological parameters.

Growth and reproduction of big sagebrush is phasic. Transpiration slows at night with the closure of stomata (Black and Mack 1986). Substantial growth occurs in the spring and early summer when water, often as snowmelt, is readily available (Caldwell et al. 1977; Comstock et al. 1988; Evans and Black 1993), even though big sagebrush is an evergreen and has physiological activity around the year (DePuit and Caldwell 1973; Pearson 1975; B.N. Smith, unpublished data). In contrast, reproductive growth occurs during the summer and fall when soil moisture is often limiting (McArthur et al. 1979; Evans and Black 1993).

Our data show that the hybrid zone and parental habitats are different as measured by the plant response to both respiration and water potential and support the general differentiation of populations across ecological gradients (Bradshaw 1984) and physiological differentiation of sagebrush taxa (K.K. Ayre and J.S. Sperry, unpublished data). These results contrast somewhat with the phenotypically plastic responses of fountain grass (*Pennisetum setaceum*) for physiological traits across an environmental gradient in Hawaii where physiological responses differed among sites without evidence of local adaptation (Williams et al. 1995).

The respiration and water potential data along with site habitat characteristics, seed germination, survivorship, growth, plant chemistry, and a variety of reproductive parameters of our reciprocal transplant gardens (Freeman et al. 1995; Graham et al. 1995; Wang 1996; Wang et al. 1997, 1998, in review; Byrd et al. in review) demonstrate the stability and vitality of the *A. tridentata* ssp. *tridentata* × *A. t.* ssp. *vaseyana* hybrid zone. The data from series of studies, in concert, are consistent with relatively higher fitness of hybrids in the hybrid zone and thus support the ecologically dependent bounded hybrid-superiority model as an explanation for the stability of this hybrid zone over the competing ecologically neutral dynamic-equilibrium model. However, we point out that the specific physiological parameter data from this study support adaptation of hybrid plants to the hybrid zone but do not reveal genotype times environment interaction as did the fitness components (germination, growth, and reproduction) of an earlier study (Wang et al. 1997).

Our data can also be used to support the importance of hybridization in the evolution and wide adaptation of the sub-

genus *Tridentatae* (= *Artemisia tridentata* and allies; see Ward 1953; Beetle 1960; McArthur et al. 1981; Shultz 1986; and Winward and McArthur 1995). Hybrid zones could have been the source for differentiation of new genetic combinations that were able to exploit the new habitats that became available with changing climates of the Pliocene when the *Tridentatae* apparently differentiated and became important landscape dominants (McArthur et al. 1981; Thompson 1991).

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