

Ecological genetics of *Bromus tectorum*

III. The demography of reciprocally sown populations

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Summary. By incorporating demographic analyses of fitness components (e.g., survival and reproduction) within a reciprocal sowing design, we tested for 3 consecutive years whether local adaptation has occurred in the alien grass *Bromus tectorum* (cheatgrass) within 7 habitats along an environmental gradient from arid steppe to subalpine forest in the Intermountain Region of western North America. Patterns of emergence and survival were strongly influenced by the local environment. In terms of survival, expression of significant local adaptation in *Tsuga heterophylla* habitat varied among years. In contrast, relative differences in flowering time among seed sources were stable across sites and years. Populations from the arid steppe were the earliest to flower; flowering was latest in populations from the mesic *Tsuga heterophylla* habitat. In terms of net reproductive rate, evidence for local adaptation in *B. tectorum* was obtained in populations from habitats representing environmental extremes: an arid, saline site dominated by the shrub *Sarcobatus vermiculatus* and clearings within the cool, mesic *Tsuga heterophylla* forest habitat. Unlike the plants introduced from other sites, members of the resident population at the *Sarcobatus* site flowered and produced seeds before soil water became limiting. In contrast, net reproductive rates in other habitats were sometimes the lowest for populations in their home site. This lack of an advantage for local populations within more environmentally moderate sites suggests that limited dispersal may restrict the rate at which superior genotypes are introduced into a particular site.

Key words: *Bromus tectorum* – Ecological genetics – Invading species – Local adaptation – Reciprocal transplants

Immigration poses hazards for plants that they would rarely encounter in their home range. Virtually overnight they face an array of new environmental challenges with

few options that would ensure survival, much less naturalization. The immigrant population may nevertheless persist because it contains at least some genotypes among the founders that are pre-adapted to the new environmental regime (Baker 1978; Burdon et al. 1981; Cavers and Bough 1985), or are able to tolerate the new range through phenotypic plasticity (Marshall and Jain 1968; Jain 1979; Hume and Cavers 1982), or both.

With such population or individual buffering (*sensu* Moran and Marshall 1981) preventing immediate extinction, local adaptation may arise among the immigrant population. Despite the intuitive appeal and ample evidence of genotypes being differentially retained in response to local selection (Heslop-Harrison 1964), the emergence of local adaptations is not assured (Antonovics 1976); genetic variation may be insufficiently large, selection may be too unpredictable or occur at a scale too fine to be tracked genetically (Hartgerink and Bazzaz 1984), or the action of selection may be swamped by gene flow (Jain and Bradshaw 1966; McGraw 1987) or weakened by phenotypic plasticity (Sultan 1987).

Unlike the usual situation for native species, the time that has been available for locally adapted populations to arise among naturalized plants can often be estimated reliably because the arrival time of the immigrants is often known (Martins and Jain 1980; Lacey 1988). Such information places a maximum limit on both the time in which geographic re-distribution could have occurred among the immigrant phenotypes and on the number of generations that have elapsed among the descendants of the founders. Repeated introductions of the species from the home range or even other new ranges is an obvious complication in understanding the time over which evolution has operated in a new range (Baker 1972; Clegg and Allard 1972; Moran and Marshall 1981; Brown and Burdon 1983).

The chronology and circumstances surrounding the entry of *Bromus tectorum* (cheatgrass) into the arid Intermountain West region of North America are better understood than for many other alien species (Mack 1986). This annual grass apparently arrived in the interior of British Columbia after 1875 but before 1889. It appeared

within 10 years at five other locations: one each in Idaho and Utah and three in the state of Washington (Mack 1981). Using electrophoretic markers, the detection of unique multi-locus genotypes within populations across western North America indicates the grass arrived through several immigrations, each independent from its earlier arrival on the eastern U.S. seaboard. Later isolated infestations of the grass may have developed from additional introductions, intra-regional transport, or both (Novak 1990).

All these early introductions occurred in the region's steppe. Although the steppe still supports the largest populations of *B. tectorum*, the grass has since colonized forest sites following land-clearing (Pierson and Mack 1990a). Dispersal to these sites is dependent largely on livestock because tracts of cleared forests are often used as summer pasture. Thus, some cleared forest sites receive a few but recurring immigrants from the steppe. Such re-supply creates the potential for gene flow between central populations in the steppe and these outlier populations (Novak 1990), thereby swamping the effects of local selection. Thus, phenotypic plasticity – already detected to varying degrees in *B. tectorum* (Palmlblad 1968; Mack and Pyke 1983; Pierson and Mack 1990a; Rice and Mack 1991b) – might account for the persistence of populations in all these habitats. Yet, two lines of evidence suggested to us that not all occupation of the new range could be explained by phenotypic plasticity alone. First, cheatgrass colonizes disturbed sites in both steppe and forest habitats that differ strikingly in soils, climate and community structure (Daubenmire 1968; Daubenmire and Daubenmire 1970) (Table 1). Secondly, glasshouse studies on cheatgrass indicate significant amounts of genetic variation within and between populations from these steppe and forest habitats (Rice and

Mack 1991a). However, extrapolation of these results to the field can be equivocal because the expression of genetic variation is often environmentally dependent (Lewontin 1974; Bazzaz et al. 1982; Heywood and Levin 1984; Sultan 1987). Consequently, we examined the sensitivity of genetic expression to environmental variation by growing populations at several different field sites. Further, the detection of genetic variation in a common garden environment, although often suggestive, does not address directly questions about the potential adaptive nature of such variation.

We tested whether local adaptations had occurred in cheatgrass along a broad environmental gradient by incorporating demographic analysis of fitness components within a reciprocal sowing design that included seven steppe and forest habitat types. This experimental approach avoids many of the pitfalls of correlation and *post facto* explanations of adaptive traits (Stearns 1976; Gould and Lewontin 1979; Harper 1982; Bradshaw 1984; Venable 1984). When combined with separate examinations of the hierarchy of phenotypic variation (Rice and Mack 1991a) and intraspecific variation in phenotypic plasticity (Rice and Mack 1991b), we predicted that a clearer picture could emerge as to the extent and nature of evolution in *B. tectorum* since its arrival in the Intermountain West.

The study areas

Bromus tectorum occurs on disturbed sites throughout much of eastern Washington and adjacent Idaho (USA) (Mack and Pyke 1983; Pierson and Mack 1990a). The wide amplitude of the physical environments among these habitats is illustrated west to east, from the central

Table 1. Climatic data from stations within the vegetation zones used in the study

Vegetation zone and location	Elevation (m)	Mean monthly temp. (°C)		Annual Ppt. (mm)
		January	July	
<i>Artemisia tridentata</i> / <i>Agropyron spicatum</i> Richland, Washington ^a	114	1.20	24.01	198
<i>Festuca idahoensis</i> / <i>Symphoricarpos albus</i> Pullman, Washington ^a	776	-2.22	19.33	531
<i>Pinus ponderosa</i> / <i>Symphoricarpos albus</i> Moscow, Idaho ^b	811	-2.28	19.33	575
<i>Abies grandis</i> / <i>Pachistima myrsinites</i> Elk City, Idaho ^b	1237	-5.56	17.11	783
<i>Tsuga heterophylla</i> / <i>Pachistima myrsinites</i> Priest River Exptl. Forest, Idaho ^b	725	-4.67	14.44	846
<i>Abies lasiocarpa</i> / <i>Pachistima myrsinites</i> Burke, Idaho ^c	1138	-5.44	15.44	1224

^a U.S. Environmental Data and Information Service (1982)

^b Average 1941–70, U.S. Environmental Data and Information Service (1982)

^c Daubenmire and Daubenmire (1970)

part of the Columbia Basin in Washington toward the Rocky Mountains in northern Idaho. Along this gradient annual effective precipitation progressively rises, while air and soil temperatures and, in turn, length of the growing season decline (Table 1). Except as specifically cited, the following synecological and environmental information for the steppe habitats is adopted from Daubenmire (1970) and for forest habitats from Daubenmire and Daubenmire (1968). Our study sites exemplified an array of seral stands in these habitat types; the steppe sites had been altered by fire, grazing, or both, within the last 40 years. The forest sites, which had all been logged, supported early seral communities without a complete forest overstory.

Artemisia tridentata–*Agropyron spicatum* habitat type

This habitat type (hereafter referred to as h.t.) includes some of the driest sites in the steppe (Table 1), and the total canopy coverage of vascular plants may be less than 100%. Moisture content of the upper dm of soil may reach about 15% during winter from a low of about 2% (often below PWP) throughout summer and early autumn (Rickard 1967). Our site was on the Arid Lands Ecology (ALE) Reserve at the U.S. Department of Energy's Hanford Reservation in Benton County, WA. and was approximately 2 km SE of the population censused by Mack and Pyke (1983). (NW1/4 SE1/4 S.2 T10N R26E Iowa Flats, WA. Quadrangle, 46°22'37" N, 119°31'08" W).

Sarcobatus vermiculatus–*Distichlis stricta* habitat type

In this habitat type, herbaceous cover is dominated by the saltgrass *Distichlis stricta* while the shrub layer is composed primarily of greasewood, *Sarcobatus vermiculatus*. Few other native species can tolerate the saline soils to which this community is restricted (Daubenmire 1970). Soil solution conductivity to a depth of 1 m may exceed 10.0 mmho/cm; soil pH within the rooting zone may exceed 9.6, indicating high Na. The highest levels of exchangeable Na (7.3 meq/100 g) occur directly beneath *S. vermiculatus* (Rickard 1965). Meteorological conditions are the same as for the *A. tridentata*–*A. spicatum* h.t. Our site in this habitat type was within 20 km of our site on the *A. tridentata*–*A. spicatum* h.t. (NW1/4 NW1/4 S.28 T12N R25E Riverland, WA. Quadrangle, 46°30'15" N, 119°42'03" W).

Festuca idahoensis–*Symphoricarpos albus* habitat type

This mesic steppe community has both high species richness and high plant productivity. Total canopy coverage of all vascular plants in undisturbed communities is about 300 percent. Moisture content of the upper soil dm may be below PWP from early June until late August (Daubenmire 1968). Our site is on the Washington State

University Biological Reserve in Whitman County, WA (8 km NW of Pullman). The site was in same location as reported for earlier censuses on this habitat type by Mack and Pyke (1983, 1984). (NW1/4 SW1/4 S.35 T16N R44E Albion, WA Quadrangle, 46°48'43" N, 117°14'04" W).

Pinus ponderosa–*Symphoricarpos albus* habitat type

This habitat type designates the driest sites in the region on which conifers may dominate. Soils in this h.t. have about the same moisture content throughout the year as on the adjacent *Festuca*–*Symphoricarpos* h.t. (Daubenmire 1968) i.e., soil drought in summer is common. Our site was established on the Washington State University Biological Reserve, approximately 1000 m from the study site on the *F. idahoensis*–*S. albus* h.t. (SE1/4 NW1/4 S.35 T16N R44E Albion, WA Quadrangle, 46°49'44" N, 117°13'45" W).

Abies grandis–*Pachistima myrsinites* habitat type

Although the forests on this h.t. lack annual extremes in either temperature or moisture (Daubenmire 1968), removal of the forest overstory by logging greatly increases the likelihood of soil drought in summer. The understory after logging is a mixture of sprawling shrubs and perennial dicots plus colonizing species such as *B. tectorum*. Our site had been logged within the last 10 years within the St. Joe National Forest in Latah County, Idaho. (SE1/4 SW1/4 S.32 T41N R3W Deary, ID Quadrangle, 46°51'00" N, 116°44'45" W).

Tsuga heterophylla–*Pachistima myrsinites* habitat type

Similar to *Abies grandis* sites this h.t. has a mesic physical environment unless the tree canopy is removed. The composition of the seral community on these sites is similar to those originally dominated by *A. grandis*. This study site in Benewah Co., Idaho was approximately 22 km NNE of the *Abies grandis* site. (NE1/4 SW1/4 SE1/4 S.25 T43N R3W Emida, ID Quadrangle, 47°02'19" N, 116°39'33" W).

Abies lasiocarpa–*Pachistima myrsinites* habitat type

This h.t. includes much of the subalpine forest in northern Idaho; sites are consistently above 1500 m. The physical environment on these sites is markedly different from that of forests at lower elevation because air temperatures are low year around and the growing season is restricted to summer. Moisture in the upper 1 dm of the soil is above PWP throughout the year (Daubenmire 1968). Our site in this h.t. was in the Mount Spokane State Park, Spokane Co., WA (SW1/4, NW 1/4 S.22 T28N R45E, Mt. Spokane Quadrangle, 47°54'40" N, 117°06'21" W).

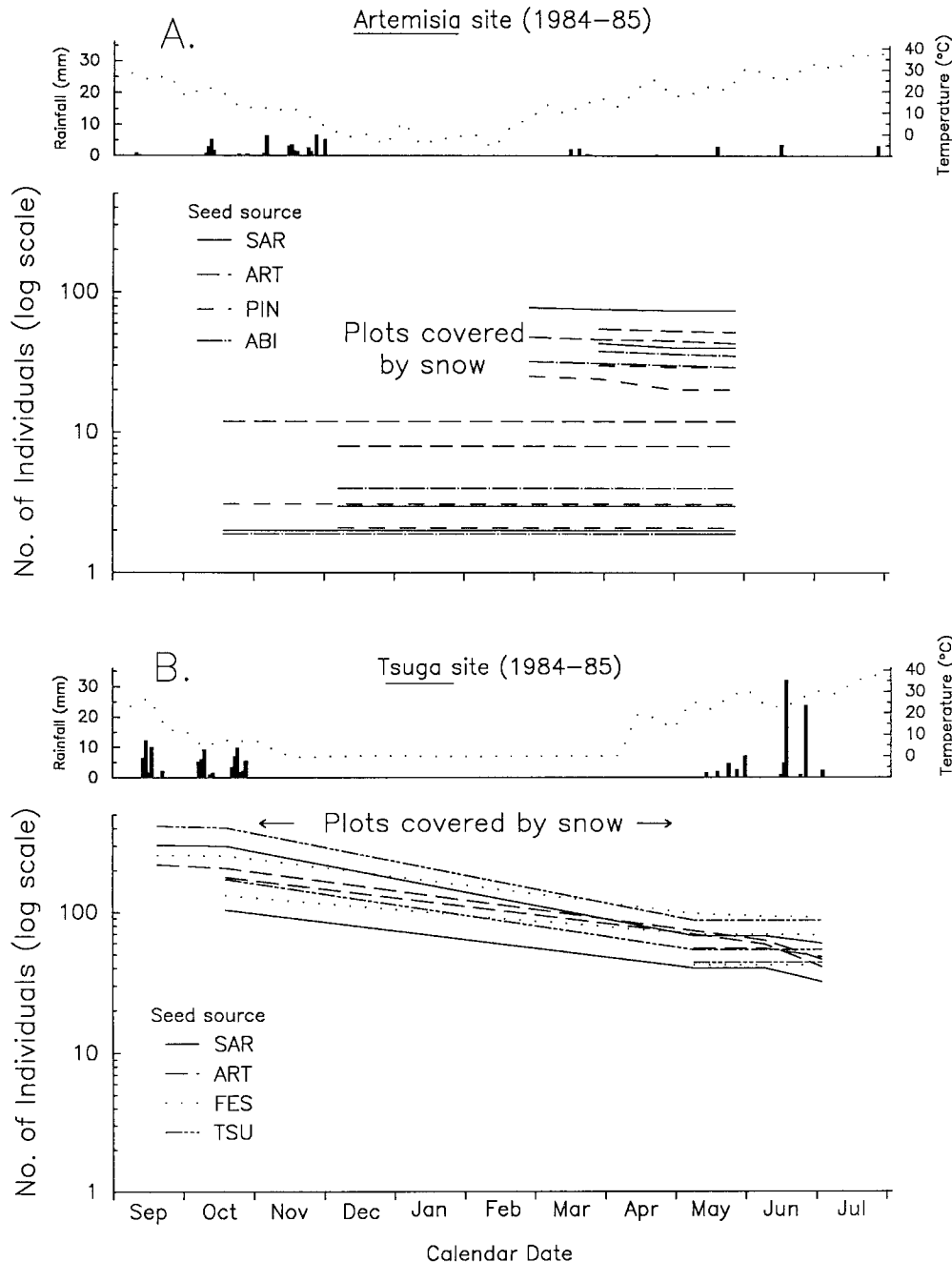


Fig. 1A–D. Survivorship curves for cohorts emergent from seeds from various sources at the *Artemisia* [(A) 1984–85; (C) 1986–87] and *Tsuga* sites [(B) 1984–85; (D) 1986–87]. Daily rainfall totals, weekly mean of the daily maximum temperature at 1 m, and duration of snow cover are indicated above each site's survivorship curves. Abbreviations for the seed sources of each cohort are *Sarcobatus* = SAR, *Artemisia* = ART, *Festuca* = FES, *Pinus* = PIN, *Abies* = ABI, and *Tsuga* = TSU. Cohorts were censused generally once a month unless covered by snow

Materials and methods

Ample seeds from the *Sarcobatus*, *Festuca*, and *Pinus* habitat types were collected on the specific study sites. Seeds from the *Artemisia* h.t. were collected 18 km NW of the study site for this h.t.: NW1/4 NW1/4 S.28 T12N R25E Riverland, WA Quadrangle, 46°30'12" N, 119°41'44" W. Seeds from the *A. grandis* and *T. heterophylla* h.t. were collected from other seral stands in those habitat types in northern Idaho: SW1/4 SW1/4 S.23 T42N R3W Deary, ID Quadrangle, 46°58'06" N, 116°41'20" W, and NE1/4 S.27 T58N R4W Prater Mountain, ID Quadrangle, 48°21'11" N, 116°49'50" W, respectively. Although *B. tectorum* occurs occasionally in the *A. lasiocarpa*-*P. myrsinites* h.t. (L.C. Hulbert, 2376, WS), no populations were found within this h.t. All seed collections were made in 1984. Each collection coincided with local seed maturation; seeds from the *Artemisia* and *Sarcobatus* sites were collected in mid to late June. Seeds from the *Festuca* and forest sites were collected in mid to late July.

Seeds were stored at room temperature in the laboratory before their return to the field. The germination rate of the seeds was tested each summer; rates consistently exceeded 90%. These initial collections were used in all field experiments. Seed lots (either 1000 or 450 seeds each) were prepared by removing plant debris and seeds obviously infected with smut. Seeds were sown at all sites in early September in each of the three years of the experiment.

Experimental plots were prepared by first clipping resident vegetation to ground level and removing the undecomposed litter. Resident seeds were killed by application of a soil sterilant (VAPAM – Stauffer Chemical Company) to each plot according to the procedure described by Pierson and Mack (1990b). The efficacy of the soil sterilant was tested by applying it to control plots, i.e., plots to which no seeds were sown. The potential emergence of residual resident seeds of *B. tectorum* was always < 1% as gauged by these control plots. Although soil sterilization obviously was not natural, it simulated the type of soil disturbance often colonized by *B. tectorum* (Daubenmire 1970).

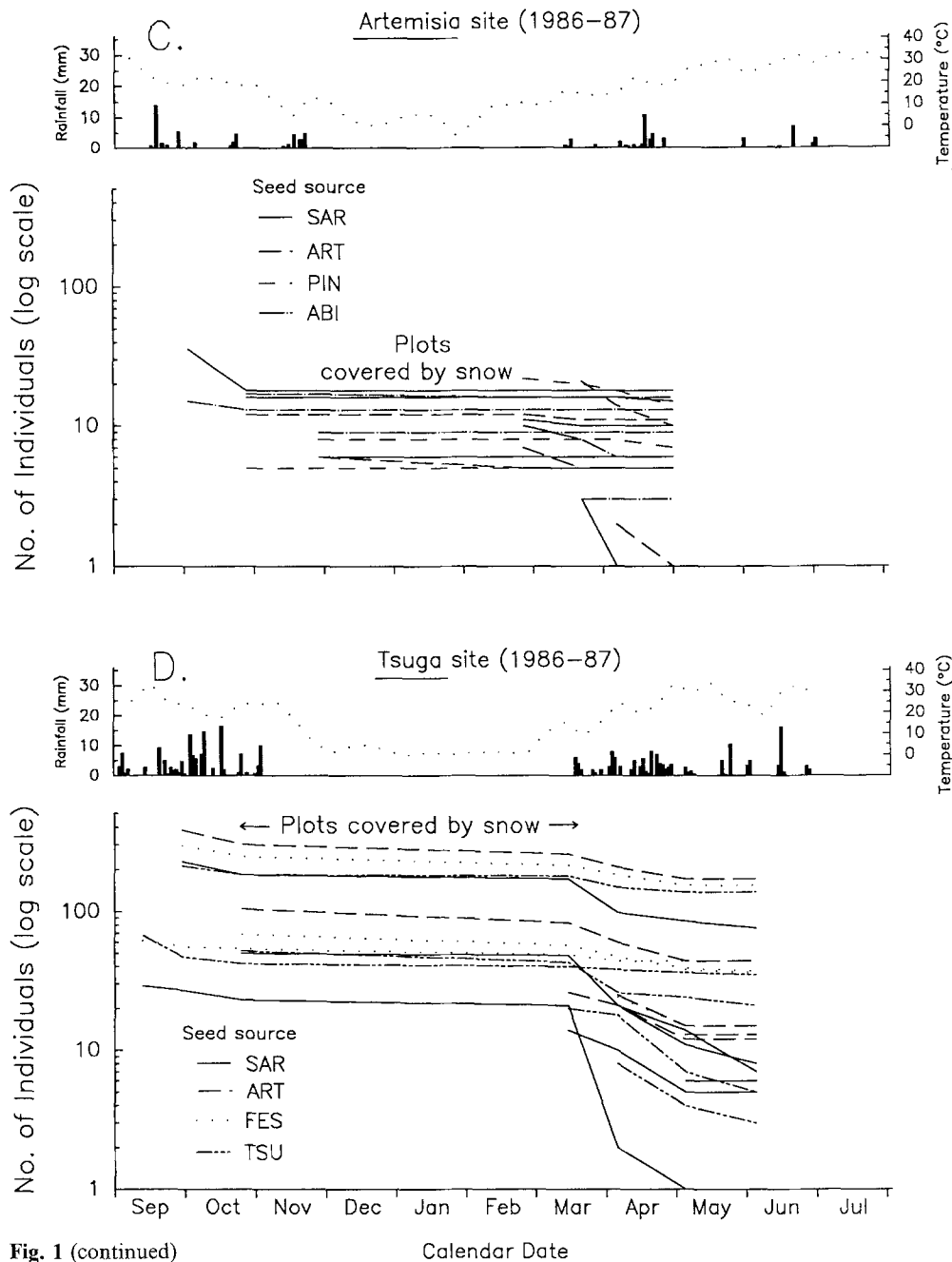


Fig. 1 (continued)

Calendar Date

The overall experimental design involved reciprocally sowing seeds from among the seven sites. To have performed all possible comparisons at all seven sites would have unnecessarily complicated execution of the experiment. Consequently, in selecting which sites would serve as the sources of seeds in each set of trials, consideration was given for comparing both the performance of populations from environmentally similar sites as well as populations from locations that represented maximum environmental differences along our regional gradient. For example, seed sources sown at the arid *Artemisia* site included seeds from the adjacent but more saline *Sarcobatus* site along with populations from the mesic *Pinus* sites and the cool sites dominated by *Abies grandis*. The *A. lasiocarpa* site received seeds from the *Artemisia* and *Festuca* habitat types only.

We employed two different procedures for assessing the performance of populations at each site. Using the procedure outlined by Mack and Pyke (1983), repeated censuses of mapped individual plants in three replicated plots were used to detect potential differences among sources in overall patterns of seedling recruitment

and survival. To increase statistical power for detecting differences among sources in survival to reproduction and reproductive output, a second series of replicated "input-output" plots (10 replicates) were established at each site. In these plots we simply measured survival to reproduction and the number of seeds produced by a known number of seeds sown in the plot the previous autumn.

Mapping plots. Plots were arranged in a randomized complete block design with seed source as the treatment; each of the plots within a block received one seed lot (approx. 1000 seeds). Treatment blocks contained either two, three or four 4×5 dm plots, and there were three blocks per site. After emergence, plants were censused monthly (except when a plot was snow covered). Emergence and death in each plot since the last census were recorded, along with notes on phenology (e.g. resumption of vegetative growth in spring and flowering time) and herbivore activity. Snow at the forest sites often prevented censusing from November until the following April. Harvesting each year progressed from site-to-site as seeds matured,

beginning in May with the *Sarcobatus* site in the arid steppe. Each plant was cut at ground level, dried (48 h at 100° C) and weighed individually. The incidence of smut infection and the weight and number of filled caryopses (i.e. seeds) were also recorded. This experimental protocol was initiated in September 1984 and repeated in September 1985 and 1986 in the same plots at each site. Following recommendations by Pyke and Thompson (1986), seedling emergence and survivorship curves of sources within each planting site were statistically compared using a Kruskal-Wallis test.

Input/output plots. This experiment also involved reciprocally sowing seeds among the seven sites. At each site in September 1985, seed lots (approx. 450 seeds each) were sown at the same density as in the mapping plots into plots arranged in a randomized complete block design with seed source as the treatment. Each treatment block contained two to four 3×3 dm plots, and there were ten blocks per site. Unlike the procedure used for the mapping plots, plants in these plots were not censused until harvest the following spring. Beginning in May at the *Sarcobatus* site we harvested the plants located in the central 2.5×2.5 dm portions of each plot. Details of the harvest follow the procedure used for the mapping plots.

In September 1984 we established micrometeorological stations at each site, except in the subalpine forest. Hourly and daily temperature (°C) was measured at 1 m and 10 cm above the soil surface and 1 cm and 50 cm below the soil surface with Fenwal UUT 51J1 thermistors. Hourly and daily precipitation (mm) was measured at 1 m above the soil surface with Edmund Scientific digital rain gauges. Data from all sensors were stored in the field on magnetic tape (Campbell Scientific CR21 Micrologger).

Results

Seedling emergence and survival. For all planting sites and all three years of the study, Kruskal-Wallis comparisons of emergence patterns and survivorship curves failed to detect significant differences ($P > 0.20$) among seed sources within a site. No attempt has been made to display detailed results on emergence patterns for all seed sources across sites and years; time of seedling emergence appeared to be determined primarily by the local patterns of temperature and precipitation at a site. Consequently, we have chosen to present representative results for contrasting sites and years: *Artemisia* and *Tsuga* sites in 1984–85 and 1986–87 (Fig. 1).

Recruitment occurred in two major periods, autumn and late winter-early spring; both periods included the emergence of multiple cohorts from each seed source. Pulses of recruitment in autumn in both steppe and forest sites followed periods of significant precipitation. With rising temperatures in late winter in both years, recruitment resumed from all seed sources in spring. Spring recruitment in forest sites lagged behind emergence in the steppe, a delay caused by both the longer time required for these forest soils to warm and for snow melt. Low temperature appears to be the main limitation for the resumption of recruitment in the spring because soil water is readily available at both steppe and forest sites in early spring. Although spring recruitment was generally small in the *Tsuga* site in both years (Fig. 1B and 1D), the amount of spring recruitment in the *Artemisia* site varied between years (Fig. 1A and 1C). For instance, in 1984–85 at the *Artemisia* site the bulk of recruitment occurred in the spring (Fig. 1A).

Similar to patterns of recruitment, survivorship was influenced by local environmental conditions each year. Substantial mortality occurred even before any plants emerged. Pre-emergence mortality in the *Tsuga* site averaged (± 1 SE) across seed sources was relatively consistent across years (51.7% \pm 5.1 in 1984–85 and 56.3% \pm 5.0 in 1986–87). Seed mortality was much higher but similarly consistent in the *Artemisia* site (90.5% \pm 1.7 in 1984–85 and 94.7% \pm 0.8 in 1986–87). The small standard errors of these mean values averaged across source populations underscore the apparent insensitivity of seed mortality to seed source.

Patterns of autumn survival at the *Tsuga* site differ between 1984–85 (Fig. 1B) and 1986–87 (Fig. 1D) in that cohorts emerging in autumn 1984 experienced little mortality until the plots were covered by snow. In contrast, before the development of persistent snow cover at the same site in autumn 1986, cohorts were often reduced by 1/3 or more. These same populations at the *Tsuga* site experienced further substantial mortality in spring, 1987. The vagaries of environment in both years caused substantially lower post-emergence mortality in the populations at the *Artemisia* site compared to populations at the *Tsuga* site. Seedling survival was especially high for all cohorts, regardless of source, at this steppe site in

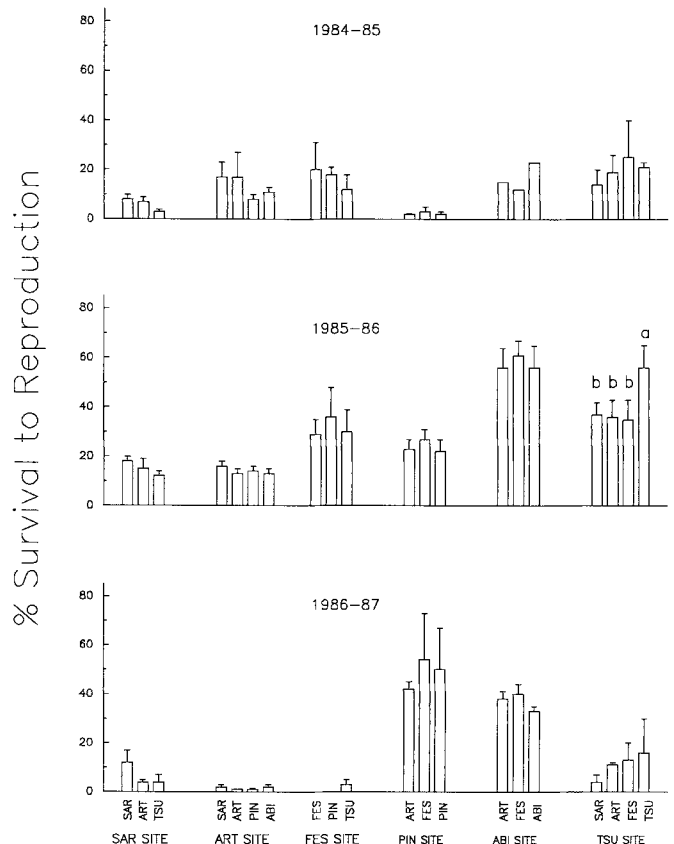


Fig. 2. Percent survival to reproduction (± 1 SE) for plants from each seed source at each site in the three years of the study. Within each site, significant ($P < 0.05$) differences in survival among seed sources are indicated with different letters; all other comparisons within each site are not significantly different. Abbreviations for all sites and seed sources are as indicated in Fig. 1

1984–85 (Fig. 1A). Even in 1986–87 (Fig. 1C), most seedlings survived to flowering.

Survival to reproduction. Survival to reproduction was often higher on our study sites within clearings in the forest habitats in comparison to the steppe habitats (e.g., 1986–87), but variation in survival to reproduction depended primarily on the interactive environmental effects of site and year (Fig 2.). For example, in 1984–85, survival across sources in the *Pinus* site was less than 10% whereas, in 1986–87 survival exceeded 45%. In contrast, survival in the adjacent *Festuca* site was negligible in 1986–87 but greater than 25% in 1985–86. The only significant ($P < 0.05$) seed source effect occurred in the *Tsuga* site in 1985–86 where survival was highest in the population from the *Tsuga* habitat type. There was total pre-reproductive mortality for all seed sources at the site within the *Abies lasiocarpa* h.t. for all three years of the study. Consequently, no data are presented from this site.

Precocity of flowering. The onset of flowering was substantially different among seed sources within each site – differences that were consistent across years (Fig. 3). Plants from the arid steppe sites (*Sarcobatus* and *Artemi-*

sia) flowered earlier than plants from other seed sources, regardless of site or year. In addition to these relative differences among seed sources in the onset of flowering, there was a progressively greater delay in anthesis along the moisture/temperature gradient from arid steppe to mesic forest sites (data not shown). No plant survived to flower in the *Festuca* site in 1986–87 because of heavy microtine grazing.

Plant size and seed production. Expression of differences among seed sources in plant size at harvest was dependent upon the interactive effects of site and year (Fig. 4). For example, at the *Artemisia* site, plants from the *Pinus* seed source were largest in 1984–85, not significantly different from other sources in 1985–86, and smallest in 1986–87. Averaged across seed source and year, there was a general tendency for plants in the arid steppe sites (*Sarcobatus* and *Artemisia*) to grow larger than plants at the mesic forest sites (*Abies* and *Tsuga*). Patterns in seed production (Fig. 5) closely paralleled those described above for plant dry weight. This outcome is not surprising because there was a strong positive correlation ($P < 0.001$) between plant dry weight and seed production (regardless of seed source) in each year of the study (1984–85, $r = 0.88$; 1985–86, $r = 0.90$; 1986–87, $r = 0.93$).

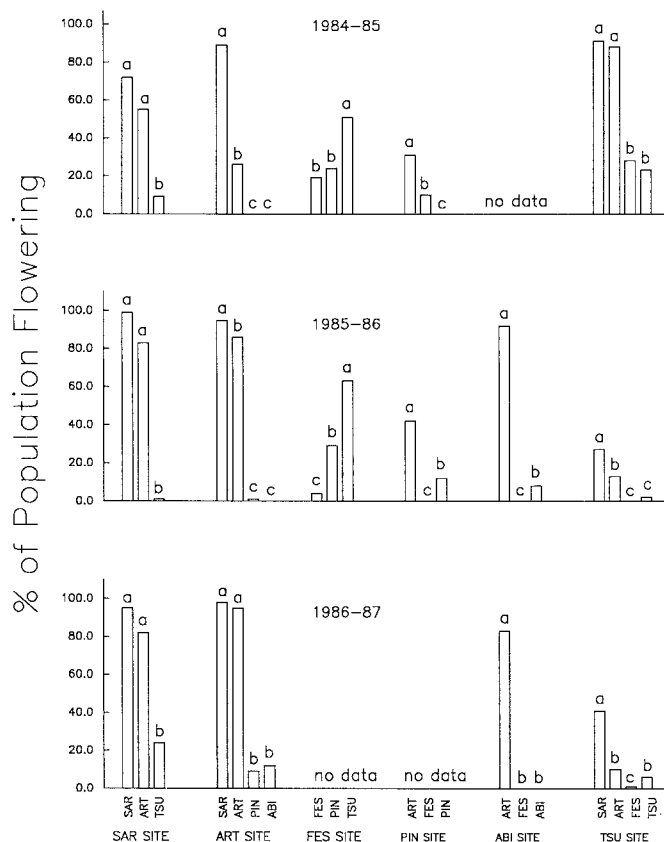


Fig. 3. Percent of adults from each source that were flowering ($x \pm 1$ SE) within a site when at least 20% of the adults from one of the seed sources had flowered. Within each site, significant ($P < 0.05$) differences in flowering among seed sources are indicated with different letters; all other comparisons within each site are not significantly different. Abbreviations for all sites and seed sources are as indicated in Fig. 1

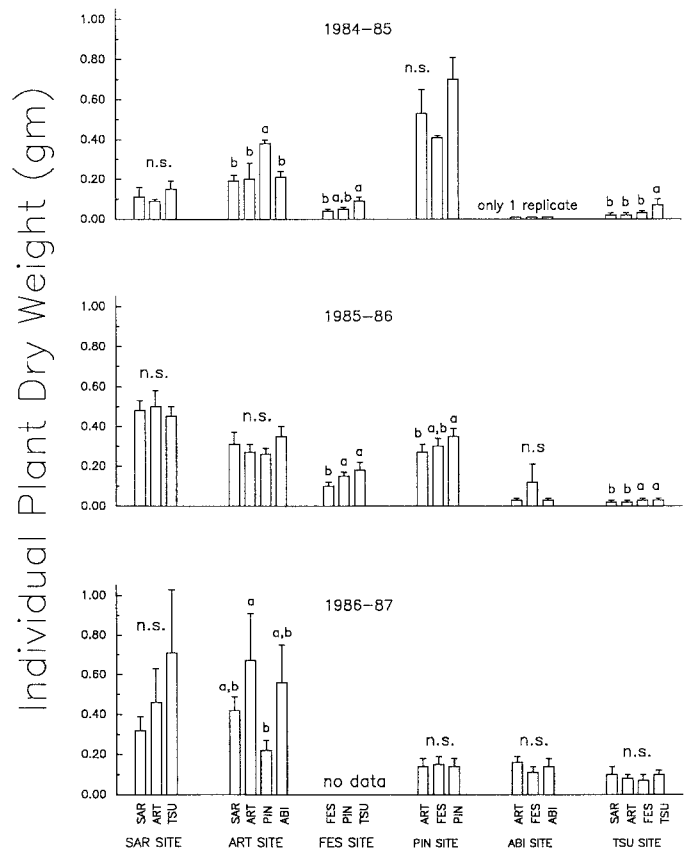


Fig. 4. Mean individual dry weight ($x \pm 1$ SE) for adult plants from each seed source at each site in the three years of the study. Within each site, significant ($P < 0.05$) differences in plant dry weight among seed sources are indicated with different letters; all other comparisons within each site are not significantly different. Abbreviations for all sites and seed sources are as indicated in Fig. 1

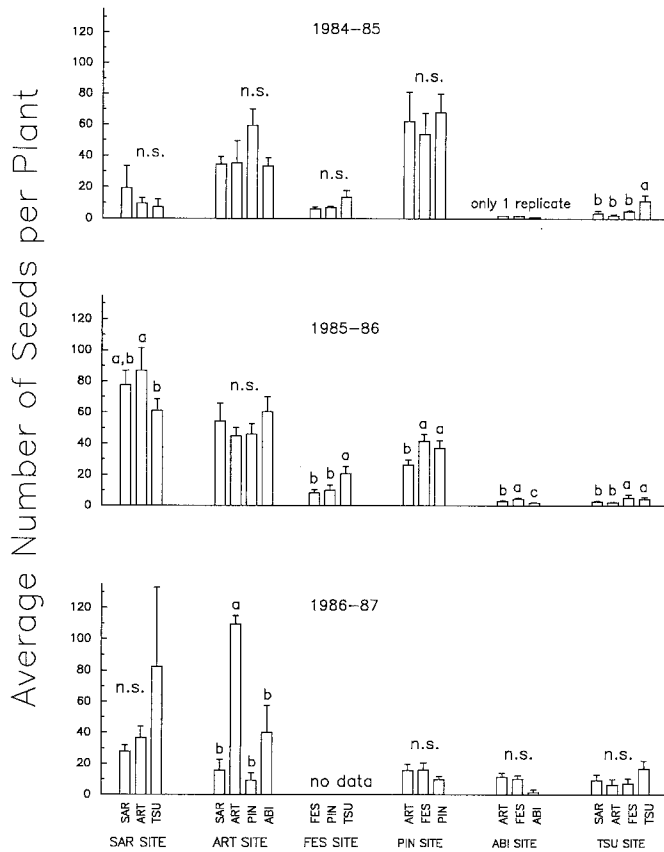


Fig. 5. Mean seed production per plant ($\bar{x} \pm 1$ SE) for adult plants from each seed source at each site in the three years of the study. Within each site, significant ($P < 0.05$) differences in seed production among plants from the various seed sources are indicated with different letters; all other comparisons within each site are not significantly different. Abbreviations for all sites and seed sources are as indicated in Fig. 1

Net reproductive rate. Similar to survival and reproduction, differences among seed sources in their population growth rates depended on both site and year (Fig. 6). Results from the environmentally extreme *Sarcobatus* and *Tsuga* sites provide evidence for local adaptation: net reproductive rates of populations from these seed sources were highest when sown on the same habitat types from which they had been collected. In contrast, a relative selective disadvantage was indicated for the *Abies* source population in its home site: it exhibited the lowest growth rate among seed sources sown at the *Abies* site in both 1985-86 and 1986-87.

Discussion

A primary goal of this study was to detect instances in which the ability of *Bromus tectorum* to persist could be related to local adaptations rather than phenotypic plasticity. This search for locally-adapted traits stemmed from our having measured substantial genetic variation among and within these same cheatgrass populations in traits affecting fitness (Rice and Mack 1991a). In contrast, the phenotypic expression of presumed genetic differences among populations within this study was

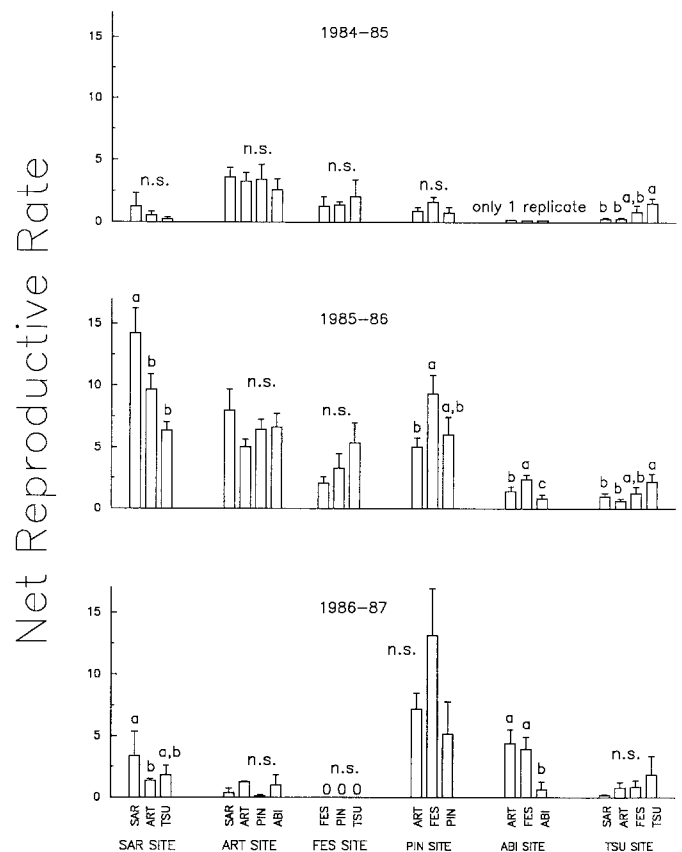


Fig. 6. Net reproductive rate ($\bar{x} \pm 1$ SE) for populations from each seed source at each site in the three years of the study. Within each site, significant ($P < 0.05$) differences in net reproductive rate among seed sources are indicated with different letters; all other comparisons within each site are not significantly different. Abbreviations for all sites and seed sources are as indicated in Fig. 1

more limited. Furthermore, detecting these differences depended on the particular site and year of measurement (cf. Davies and Snaydon 1976; Schmidt and Levin 1985). Consistent indications of local adaptation were found only in the two most extreme habitat types along the environmental gradient; the saline arid steppe *Sarcobatus vermiculatus* h.t. and the cool, mesic *Tsuga heterophylla* h.t.. It is undeniable that under controlled growing conditions considerable precision is possible for detecting genetic variation in traits of potential adaptive significance (Schaal 1984). However, comparison of the results from our glasshouse and field studies reinforces the contention that, although the potential for ecotypic variation and evolutionary change can be studied within a common garden or glasshouse environment, its demonstration requires a reciprocal transplant experiment in the field (Antonovics and Primack 1982; Venable 1984). As emphasized by Sultan (1987), if ecotypic differences are discernable only under the controlled conditions within a common garden, then the relevance of this variation under natural conditions is equivocal. Genetic variation undetectable by the investigator in the field may be also invisible to natural selection.

Phenotypic expression of genetic variation in general, and local adaptation in particular, depended in this study

on both the sowing site and the trait under study. A comparison of the results for flowering phenology and emergence patterns provides a contrast between two traits in the degree of apparent genetic differentiation among populations. Phenotypic differences in flowering time among the different source populations were consistent regardless of planting site or year with the arid steppe populations always flowering earlier than the forest populations. Very early flowering in the *Sarcobatus* populations may represent an adaptive response to the annual decline of soil moisture on these saline sites. The vigor of *B. tectorum* on these sites may be in response to soil moisture in winter which exceeds that available on *Artemisia* sites (Rickard 1967). Despite comparatively higher availability of soil moisture in winter and early spring, moisture content in these saline soils can fall below permanent wilting point by early April, a full month before wilt occurs on the zonal soils in the *A. tridentata* h.t. (Rickard 1967). Precocious flowering in the *Sarcobatus* populations may thus contribute to local adaptation (as measured by net reproductive rate) in this population.

The adaptive significance of such precocious flowering has been seen repeatedly among both wild and agronomic species in saline or xeric environments. In California annual grasslands, populations of the native grass *Festuca microstachys* have genetically differentiated in flowering phenology so that populations from drier sites flower earlier (Kannenberg and Allard 1967). Similarly, in serpentine populations of the annual *Linanthus androsaceus*, Schmitt (1985) proposed that drought, rather than pollinator availability, was the major selective factor causing earlier flowering in serpentine compared to non-serpentine populations. Instead of selecting for physiological drought resistance, Fanous (1967) concluded that more progress in breeding pearl millet (*Pennisetum typhoideum*) for arid lands could be made by selection for early maturity to avoid, rather than tolerate, drought.

In contrast to this strong indication of genetic variation in flowering time, cheatgrass seedling emergence varied among sites and years but did not display any differences among the various seed sources. This apparent lack of genetic differentiation in patterns of seedling emergence has been noted previously for other species (Arthur et al. 1973; Kalisz 1986; Cheplick 1988; Lacey 1988). For instance, in *Papaver dubium*, heritability for variation in autumn and spring emergence is nil (Arthur et al. 1973). The low heritabilities for germination timing reported for *Collinsia verna* were thought to reflect the action of stabilizing selection on the optimum date of germination (Kalisz 1986).

In our study, environmental effects were also of primary importance in determining the probability of cheatgrass survival to reproduction. With the exception of plants at the *Tsuga* site in 1985–86, survival was determined largely by the interaction of site and year with little indication of seed source effect. This strong influence of environment on seedling emergence and plant survival emphasizes the potential importance of plastic demographic responses to resource variability; in

heterogeneous environments, genetic bases for variation in fitness can be overwhelmed by environmental determinants of fitness (Hartgerink and Bazzaz 1984). It further suggests that large year-to-year differences in the demography of *B. tectorum* observed by Mack and Pyke (1983) on zonal soils in the steppe were due largely to environmental rather than genetic factors. Although trends in cheatgrass survivorship within the *Sarcobatus* and *Tsuga* sites suggest local adaptation, the evidence for such adaptation is not as pronounced as reported elsewhere for transplanted seeds (Schemske 1984; Schmidt and Levin 1985; Davy and Smith 1985; Waser and Price 1985).

None of the populations we examined persisted at the *A. lasiocarpa* site, although clearcuts within this subalpine habitat are apparently within the range of phenotypes not included within our study. Plants with filled caryopses are occasionally found in this zone in the conterminous U.S. (L.C. Hulbert, 2376, WS), and the grass has been reported from Alaska and the Yukon (Hulten 1968). Furthermore, such records of small, isolated populations of cheatgrass mirror its tenuous status in the European subalpine (Hess et al. 1967). Cheatgrass may be extending its North American range simultaneously at high elevation and latitude, similar to the current, northward spread of *Sorghum halepense* and *Datura stramonium* in eastern Canada (Warwick et al. 1984; Weaver et al. 1985).

Differences among source populations in seed number per plant depended on both site and year. In studies of the relative contribution of genetic and plastic responses to geographic differentiation in the congener, *Bromus rubens*, phenotypic variation in reproductive traits such as panicle weight and seed weight similarly depended on the interaction of seed source and the plant's growing environment (Wu and Jain 1978). Even in the *Sarcobatus* and *Tsuga* sites where local adaptation was detected, the magnitude of the differences in fecundity varied among years. The general importance of year-to-year environmental variation on the expression of genetic differences in fecundity is difficult to estimate because few reciprocal transplant studies on annuals are conducted for more than one year. An exception is a two-year study of *Phlox drummondii* in which phenotypic expression of population effects on fecundity and local adaptation were also found to be highly dependent on year as well as planting site (Schmidt and Levin 1985).

Using net reproductive rate as an integrative index of fitness, indications of local adaptation were most pronounced at the environmentally extreme habitats: the driest and most saline desert steppe site (*Sarcobatus vermiculatus* h.t.) and the coolest, most mesic forest site (*Tsuga heterophylla* h.t.). Selective differentials indicating local adaptation at these sites were consistent (if not always significant) across the three years of the study. Consistency of selective differentials, although not often reported, is an important determinant of the probability of genetic differentiation among populations (Sultan 1987). The detection of local adaptation in these contrasting sites suggests that plastic responses alone may be insufficient to allow persistence of cheatgrass in habitats

representing the environmental extremes of its new range. Furthermore, selection by the physical environment was partially predictable by habitat type (*sensu* Daubenmire and Daubenmire 1968). The seed source for *B. tectorum* from the *Tsuga* h.t. was collected 270 km N of the *Tsuga* site used in the reciprocal sowing experiment. Yet at the *Tsuga* site the plants from this seed source still displayed a selective advantage compared to other populations. Apparently local adaptation has been to the general environment characterizing the *Tsuga heterophylla* h.t. and not just to a particular site within this habitat type.

In addition to their physical environments, the *Sarcobatus* and *Tsuga* sites also differ markedly in the degree to which the populations at each site are isolated from other cheatgrass populations. Because the *Sarcobatus* and *Artemisia* seed sources are within 100 m of each other, the potential for gene flow to reduce genetic differentiation between these two populations is likely to be high. The consistent indication of local adaptation of cheatgrass in the *Sarcobatus* site in spite of potential gene flow suggests that selective forces within the *Sarcobatus* site are strong. In contrast, the relative isolation of the cheatgrass seed source at the *Tsuga* collection site would reduce the potential swamping effects of gene flow so that relatively weak selective forces would be sufficient to maintain genetic differences.

The importance of evolutionary forces other than selection, such as gene flow or genetic drift, is suggested by the relative selective disadvantage of the *A. grandis* seed source in its home site. In both years when the effect of seed source could be analyzed statistically within the site, plants collected in this h.t. had the lowest net reproductive rate of the populations tested. This apparent lack of local adaptation suggests that the vagaries of dispersal and genetic drift may have limited the rate at which superior genotypes are introduced and established within a particular site. Selfing followed by drift, rather than local natural selection, has been previously suggested as a potentially important differentiating mechanism in inbreeding annuals (Jain and Rai 1974; Schemske 1984).

Although the population from the *A. grandis* h.t. provides the clearest example of an apparent lack of local adaptation, nonadaptation was not unique to this population. There is no indication of local adaptation for any of the other populations within the three years of the study if the results from the environmentally extreme *Sarcobatus* and *Tsuga* sites are excluded. Similar instances of nonadaptation have been reported for other native and introduced plant species that colonize disturbed or successional environments (Antonovics and Primack 1982; Cheplick 1988; Rapson and Wilson 1988). Except in extreme sites where selection may be more deterministic, fine-scale and unpredictable environmental heterogeneity when combined with the enormous reproductive plasticity of cheatgrass (Palmblad 1968; Rice and Mack 1991b) may be sufficient to buffer sub-optimal genotypes against selective elimination. Perhaps part of the elusive answer to the search for those features common to naturalized species (Groves 1986; Gray 1987) is this ability to persist without the emergence of

locally adapted populations; species so endowed defy the odds against persistence in a new range.

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