# PLASTICITY AND GENETIC DIVERSITY MAY ALLOW SALTCEDAR TO INVADE COLD CLIMATES IN NORTH AMERICA

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*Abstract.* Two major mechanisms have been proposed to explain the ability of introduced populations to colonize over large habitat gradients, despite significant population bottlenecks during introduction: (1) Broad environmental tolerance—successful invaders possess life history traits that confer superior colonizing ability and/or phenotypic plasticity, allowing acclimation to a wide range of habitats. (2) Local adaptation—successful invaders rapidly adapt to local selective pressures. However, even with bottlenecks, many introduced species exhibit surprisingly high levels of genetic variation and thus the potential for evolutionary increases in invasive traits and plasticity. Here we assess the invasive potential of *Tamarix ramosissima*, by examining the degree of genetic differentiation within and among populations from the latitudinal extremes of its introduced range. Using growth chamber experiments we examined ecologically important variation in seedlings, both in trait means and their reaction norms across temperature environments. Although we found no genetic variation for gas exchange traits, within or among populations, we did find significant genetic variation for growth traits, both in the trait means and in the degree of plasticity in these traits. Northern ecotypes invested more in roots relative to southern ecotypes but only under low temperatures. Both ecotypes increased shoot investment in warm temperatures. Increased root investment in cold temperatures by northern ecotypes may increase their first winter survival. Genetic differences in seedling root investment may contribute to the ability of this species to successfully tolerate and invade a broader latitudinal range. Our data support a model in which both plasticity and adaptive evolution can contribute to the invasive potential of introduced species.

*Key words: ecological genetics; ecotypes; invasive potential; invasiveness; local adaptation; plasticity; root mass ratio; saltcedar;* Tamarix ramosissima.

## INTRODUCTION

What is the eventual fate of introduced species? Which ones will survive and flourish? From an evolutionary perspective, species introductions are essentially human caused migration events, where individuals are translocated to a novel environment. Once introduced, some species survive and establish self-sustaining populations in the novel habitat. A subset of these species may not only survive in their new habitat, but become invasive, dominating the new community and even causing the extinction of natives through rampant growth and/or indirect effects. In an effort to predict the invasive potential of exotic species attempts have been made to identify traits associated with invasiveness in plant species, but little consensus has emerged (Goodwin et al. 1999, Mack et al. 2000).

In addition to intrinsic site susceptibility to invasion, the ability of an introduced species to successfully tolerate and invade broad geographic areas has been re-
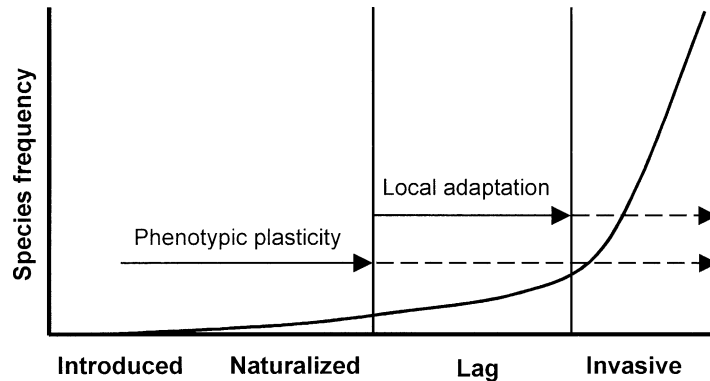
lated to two main mechanisms: broad environmental tolerance and local adaptation (Schlichting 1986, Williams and Black 1993). We use a conceptual model of invasion (Fig. 1), which incorporates both plasticity and adaptation of introduced species, and may help to explain the often large time lag between species introduction and invasion (Baker 1986, Ellstrand and Schierenbeck 2000). Plasticity may initially allow introduced species the environmental tolerance to become naturalized across a range of environments (Baker 1974). Once naturalized, recombination of genetic variation among introduced individuals can provide a range of heritable phenotypes to respond to local selection pressures and produce offspring with higher fitness (Ellstrand and Schierenbeck 2000). We argue that invasive potential can sometimes be viewed as a suite of evolutionarily labile traits, and thus attempts to predict which species are likely to become invasive based on current trait means or characters alone may be misleading (Rejmánek and Richardson 1996, Williamson and Fitter 1996a, Goodwin et al. 1999, Mack et al. 2000). We assert that non-native species (as with native species) that appear to be less noxious cannot be assumed to remain so because their invasive potential may increase during the apparently stable naturalization phase via microevolutionary processes.

It is clear that, given strong selection and ample ge-

FIG. 1. Hypothetical time course for the frequency of an invasive species. Initially, phenotypic plasticity may increase the range of habitats into which the introduced species can become naturalized. Once the species is naturalized, local selection may favor a subset of the introduced genotypes. Eventually a combination of founder effects, gene flow, mutation, and recombination may create individuals in the newly naturalized population with a phenotype closer to the optimum for the novel habitat. In some cases, adaptive evolution may lead to an increase in plasticity for some traits, and to an increase in "invasiveness" in the introduced population. For species that have been subject to multiple introductions, the potential for invasiveness (or local adaptation) to evolve rapidly may be great.

netic variation, populations become locally adapted (Antonovics 1976). Local adaptation is well documented in native plant populations on a variety of spatial scales (Jain and Bradshaw 1966, Linhart and Grant 1996). Once naturalized, introduced populations will experience new local selection pressures. Although species introductions often involve population bottlenecks, non-native species sometimes exhibit surprisingly high levels of genetic variation (Barrett and Richardson 1986). Such variation may actually increase through hybridization events (Ellstrand and Schierenbeck 2000). With ample genetic variation, adaptation has been predicted to be an important mechanism for rapid spread into multiple environments. In fact, species introductions into novel environments provide examples of some of the most rapid rates of presumably adaptive evolution (Gingerich 1983, Huey et al. 2000). Ecological genetic studies in non-native populations provide numerous examples of population differentiation across climatic, biotic and abiotic gradients (Clausen et al. 1948, Jain and Martins 1979, Martin and Harding 1980, Hume and Cavers 1982, Lacey 1988). For example, in the recently introduced annual plant, *Bromus tectorum*, in the United States, genetic differences among invasive populations suggest local adaptation via drought avoidance (Rice and Mack 1991, Rice et al. 1992).

Phenotypic plasticity provides a mechanism by which species can tolerate wide environmental variation without genetic change (Via 1994). Plasticity clearly contributes to invasive ability in genetically uniform "weeds" inhabiting wide climate ranges (Williams et al. 1995). In addition to allowing a single genotype to acclimate to multiple environments, plasticity can also buffer existing genetic variation from selection (Baker 1974, McGraw 1987, Schlichting 1986, Sultan 1987). Yet, plasticity itself is not fixed. As a mechanism for tolerance, plasticity can evolve due to natural selection (Via et al. 1995) given genetic variation in the degree of plasticity (Falconer 1990). We believe this is very important for the ecology of invasion. Genetic differences in plasticity can be rep-

resented by: different norms of reaction (Falconer 1990) evidenced by significant genotype by environment interaction (Fry 1992), or a genetic correlation of a character across environments that is less than one (Stearns 1989, Falconer 1990). As with genetic differences in trait means, the ability of genotypes to be plastic cannot be assumed to be adaptive. However, the high degree of plasticity in ecophysiological traits is hypothesized to be an adaptation for dealing with environmental heterogeneity (Bell and Lechowicz 1994).

The relative contribution of phenotypic plasticity and adaptation to invasiveness has received little attention. Here we use ecological genetics to examine invasive potential in the exotic invasive shrub saltcedar (*Tamarix ramosissima* Ledeb.). Saltcedar is native to Eurasia where it occupies lakeshore, marsh, river, and steppe habitats (Baum 1978). Because it is so aggressive in riparian ecosystems of the southwestern United States, research has focused on identifying traits of saltcedar that aid in its invasive and competitive ability (Busch and Smith 1995, Sala et al. 1996, Cleverly et al. 1997, Smith et al. 1998). In its native range, saltcedar maintains an enormous distribution across the breadth of Eurasia, from Turkey to North Korea, from Iran to Ukraine (see Baum 1978). Consistent with its broad latitudinal native distribution, saltcedar occupies the latitudinal breadth of the western contiguous U.S. (see map in Brock 1994), and it has spread throughout the northern United States since the 1960s. However, in colder areas it appears to be less invasive than in the Southwest (Lesica and Miles 2001). It is likely that multiple introductions of saltcedar in North America (Robinson 1965) from different regions of its large native range have resulted in considerable genetic variation available for adaptation in these non-native populations.

If non-neutral genetic variation exists across habitats, it can contribute to local adaptation in the new range of distribution of this species. Temperature has strong effects on plant growth and survival, limiting ecotype and species distributions (Berry and Bjorkman 1980, Berry and Raison 1981, Woodward 1986). There-

PLATE 1. Saltcedar seedlings emerging within an environmental chamber approximating summer growing conditions in southern Arizona. Photograph by Jason P. Sexton.

fore, a latitudinal gradient should represent a selective gradient for saltcedar due to temperature and growing season differences. For instance, seedlings at colder, northern latitudes with shorter growing seasons are less developed when they overwinter, leading to high seedling mortality. We measured genetic variation in functional trait means and reaction norms of saltcedar across two temperature treatments. To determine the potential of saltcedar to use plasticity and local adaptation to increase its invasiveness in the wide range of habitats to which it has become naturalized we asked: (a) Does genetic variation exist for functional traits within and among non-native populations of saltcedar? (b) Does a genotype by environment interaction exist for these responses? (c) If so, do these responses fit a model of functional, invasive ecotypes for respective populations?

## MATERIALS AND METHODS

### Climates and sampling

We sampled populations at the extremes of the latitudinal range of saltcedar in the western United States. Seeds were collected in June and July 1998 in each of three riparian populations in southern Arizona and eastern Montana. To account for possible population structuring, populations within these regions were delineated as stands of saltcedar at a minimum distance of 10 km from each other. Seeds were collected randomly from five plants at each population for a total of 15 families from each region. A family consists of a seed set derived from a single plant in the field. Seed source populations from Arizona and Montana will hereafter be referred to as Southern and Northern, respectively.

Southern populations were sampled along the Gila River within lower Sonoran bajada habitat, a drainage historically dominated by *Populus fremontii*, *Salix goodingii*, and *Prosopis velutina* (Haase 1972). This low elevational gradient portion of the Gila River, now dominated by near-monospecific stands of saltcedar,

has been subjected to myriad human disturbances including clearing for agriculture, water diversion, and flood control (Minckley and Brown 1994). Seed production at these sites can occur over half the year, from May to October (Warren and Turner 1975). Southern seeds were collected at three locations: 33°20.5′ N, 112°37.5′ W; 33°22.7′ N, 112°19.5′ W; 33°15.2′ N, 112°09.7′ W. Nearby Buckeye, Arizona, experiences an average of 344 frost-free days, with June–August having Min./Max. air temperatures of 22.4°/41.9°C, and an overall mean of 32.1°C for that period (Garwood 1996).

Northern populations were sampled within the Great Plains along low elevational gradient stretches of the Yellowstone and Bighorn rivers at similar elevations within a distance of 50 km. These sites are dominated by *Populus deltoides*, *Salix exigua*, *Shepherdia argentea*, and *Symphoricarpos occidentalis* (Hansen et al. 1995). At these sites, saltcedar occurs mostly in discrete patches or stands within 100 m of the main channel and on river channel islands. Saltcedar commonly occurs at these sites where disturbances of grazing, development and flooding are apparent. Seed production at these sites occurs from late June through September. Northern seeds were collected at three locations: 46°08.4′ N, 107°27.8′ W; 45°50.6′ N, 107°35.2′ W; 46°15.4′ N, 107°20.3′ W. Nearby Hysham, Montana, experiences an average of 191 frost-free days, with June–August having Min./Max. air temperatures of 11.6°/29.8°C, and an overall mean of 20.7°C for that period (Garwood 1996).

### Growth chambers

Saltcedar plants were grown within two controlled environmental chambers (EGC Plant Growth Chambers, Chagrin Falls, Ohio) in 14-h days, 10-h nights under a mixture of incandescent and fluorescent lights (400–550 $\mu$mol photons·m$^{-2}$·s$^{-1}$) (see Plate 1). Seeds were germinated in water for 2 d and then transferred

to mesh-bottom PVC plastic pipes (5 cm diameter $\times$ 1 m height, to accommodate the future tap root) filled with 2.0 L of moderate coarsity silica sand (0.58-mm grains in the upper 5 cm, and 0.20-mm grains below). Germination conditions were 12°/20° and 15°/20°C (night/day) in the low- and high-temperature chambers, respectively. Germinated seeds were transplanted such that each chamber contained seeds from the two regions $\times$ three populations per region $\times$ five families per population $\times$ ten replicates per family for a total of 300 plants (600 plants for the experiment). Plants were arranged into five experimental blocks per chamber, each block containing two randomly positioned representatives of each family to account for within treatment heterogeneity (Potvin and Tardif 1988). Pipes were capped with transparent plastic cups for two days after planting to avoid desiccation of seedling roots at the soil surface. Growth conditions in the two chambers were diverged gradually over two weeks to represent Southern (20°/37°C) and Northern (11°/25°C) field conditions. Emerging seedlings were thinned to one per PVC pipe. Soil moisture was held near saturation during seedling onset (2 wk) and sand was kept moist during the remainder of the growth period by partially submerging the pipes to half their height in plastic tanks. Plants were watered daily and fertilized every two weeks with Peters 20-20-20 NPK fertilizer (W. R. Grace, Fogelsville, Pennsylvania) throughout the experimental period. Temperature and relative humidity at plant canopy height were continuously monitored throughout the experiment with a CR10X data logger (Campbell Scientific, Logan, Utah). Daytime vapor pressure deficits of the air in the chambers were 1.3 and 3.4 kPa in the low- and high-temperature chambers, respectively.

### Gas exchange

After 99 d of growth we measured net photosynthetic rate ($A_n$) and stomatal conductance ($g$) from one block (60 plants) in each chamber using a LI-COR 6200 portable photosynthesis system (LI-COR, Lincoln, Nebraska). Mean air temperatures during gas exchange measurements were 23° and 35°C in the low- and high-temperature chambers, respectively. Transpiration rate ($E$) was calculated from $g$ and independent measurements of air temperature and relative humidity, assuming similar air and leaf temperatures. Instantaneous water-use efficiency (WUE$_{inst}$) was calculated from measurements of $A_n$ and $E$. Gas exchange parameters were expressed on a leaf dry mass basis.

### Growth and biomass allocation

After 86 d plants were harvested one block at a time over a 21-d period. Roots and shoots were washed, separated, then oven dried for a minimum of 48 h at 60°C. Dried roots and shoots were weighed separately and total plant masses were calculated for each individual. Shoot and root lengths were measured at time

TABLE 1. Summary of analysis of variance for temperature responses of *Tamarix ramosissima* within growth chambers for gas exchange traits: net photosynthesis on a dry mass basis ($A_n$), stomatal conductance ($g$), transpiration ($E$), and instantaneous water-use efficiency (WUE$_{inst}$).

| Dependent variable | Type III ss | df | F | Significance |
|---|---|---|---|---|
| **Temperature** | | | | |
| $A_n$ | 214 441.415 | 1 | 7.474 | 0.008 |
| $g$ | 7.811 | 1 | 30.594 | 0.000 |
| $E$ | 13.658 | 1 | 78.430 | 0.000 |
| WUE$_{inst}$ | 5.268 | 1 | 33.998 | 0.000 |
| **Region** | | | | |
| $A_n$ | 29 073.926 | 1 | 1.194 | 0.281 |
| $g$ | 0.204 | 1 | 1.623 | 0.208 |
| $E$ | 0.361 | 1 | 3.781 | 0.058 |
| WUE$_{inst}$ | 0.06878 | 1 | 0.665 | 0.419 |
| **Family** | | | | |
| $A_n$ | 685 748.867 | 29 | 0.824 | 0.715 |
| $g$ | 3.048 | 29 | 0.412 | 0.995 |
| $E$ | 2.407 | 29 | 0.477 | 0.986 |
| WUE$_{inst}$ | 2.762 | 29 | 0.615 | 0.928 |
| **Region $\times$ Temperature** | | | | |
| $A_n$ | 20 744.449 | 1 | 0.723 | 0.398 |
| $g$ | 0.03798 | 1 | 0.149 | 0.701 |
| $E$ | 0.007872 | 1 | 0.045 | 0.832 |
| WUE$_{inst}$ | 0.02869 | 1 | 0.185 | 0.668 |

*Notes:* Results are from four separate ANOVAs (one for each trait). In this mixed model randomized block design, family is a random factor nested within region. Data for $g$, $E$, and WUE$_{inst}$ were log transformed before analysis.

of harvest. In addition we calculated root mass ratio (RMR), as the root mass divided by total mass.

### Statistics

Data were analyzed using analysis of variance (procedure GLM, in the SAS statistical package, version 6.12 [Freund et al. 1991]). Because we were primarily interested in among region differences, the effect of region was considered a fixed factor and family was considered a random factor nested within region. Population, nested within region, was initially included in the analysis but was excluded because it did not improve model fit. Because whole blocks were harvested at once, the effect of block is confounded by the effect of harvest date and thus we used harvest date as a covariate. Due to non-normality (skewness), data were natural log and cube root transformed to meet the assumptions of parametric analysis.

### RESULTS

### Gas exchange

We did not find evidence for genetic variation at local (i.e., a significant effect of family or population) or regional spatial scales in gas exchange traits ($P > 0.05$ for family and region effects; Table 1). A lack of any significant effect of family or population may be partly due to the reduced sample size for these traits. Due to a lack of genetic effect we pooled all data to examine

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TABLE 2. Summary of analysis of variance for temperature responses of *Tamarix ramosissima* within growth chambers for growth traits.

| Dependent variable | Type III ss | df | F | P |
|---|---|---|---|---|
| Harvest time (covariate) | | | | |
| RMR | 1.33 | 1 | 32.62 | 0.00000005 |
| Total mass | 17.366 | 1 | 41.39 | 0.0000000005 |
| Root mass | 28.309 | 1 | 50.84 | 0.0000000005 |
| Shoot mass | 13.014 | 1 | 32.84 | 0.00000005 |
| Shoot length | 3.819 | 1 | 30.55 | 0.00000005 |
| Temperature | | | | |
| RMR | 9.337 | 1 | 228.93 | 0.0000000005 |
| Total mass | 53.139 | 1 | 126.67 | 0.0000000005 |
| Root mass | 17.927 | 1 | 32.20 | 0.00000005 |
| Shoot mass | 75.496 | 1 | 190.52 | 0.0000000005 |
| Shoot length | 30.912 | 1 | 296.13 | 0.0000000005 |
| Region | | | | |
| RMR | 0.321 | 1 | 2.24 | 0.15 |
| Total mass | 0.170 | 1 | 0.18 | 0.7 |
| Root mass | 0.957 | 1 | 0.68 | 0.5 |
| Shoot mass | 4.484E-03 | 1 | 0.01 | 0.95 |
| Shoot length | 0.929 | 1 | 4.07 | 0.06 |
| Family | | | | |
| RMR | 4.023 | 28 | 3.52 | 0.000000005 |
| Total mass | 25.999 | 28 | 2.218 | 0.0005 |
| Root mass | 39.583 | 28 | 2.54 | 0.0005 |
| Shoot mass | 22.702 | 28 | 2.05 | 0.005 |
| Shoot length | 6.426 | 28 | 2.20 | 0.0005 |
| Region × temperature | | | | |
| RMR | 0.688 | 1 | 16.86 | 0.00005 |
| Total mass | 0.378 | 1 | 0.90 | 0.35 |
| Root mass | 4.610E-02 | 1 | 0.08 | 0.78 |
| Shoot mass | 1.094 | 1 | 2.76 | 0.1 |
| Shoot length | 7.292E-02 | 1 | 0.70 | 0.5 |

*Notes:* The interaction between region and temperature for the trait root mass ratio (RMR) was significant. Data were analyzed using a mixed model (randomized block design), where family was considered a random factor nested within region. Harvest time was used as a covariate within this model. Data were transformed prior to analysis to improve normality: shoot mass, root mass, total mass, and RMR were natural log transformed; shoot length was cube root transformed. Results are from five separate ANOVAs (one for each trait).

phenotypic plasticity in these traits as a function of temperature. All gas exchange variables (means $\pm$ 1 SE) differed significantly between the high- and low-temperature environments (Table 1). Higher temperature increased $A_n$ by 21.5% ($P = 0.008$), $E$ by 122.6% ($P < 0.001$), and $g$ by 189% ($P < 0.001$), and decreased $WUE_{inst}$ by 33.3% ($P < 0.001$).

### Growth and biomass allocation

Like the gas exchange parameters, all growth traits changed significantly with temperature. Unlike gas exchange, we found evidence for genetic variation in growth traits. The effect of family nested within region was significant for all traits (Table 2), indicating that genetic variation exists within regions. The effect of region was marginally significant only for shoot length ($P = 0.06$) with longer shoots for Southern seedlings

in both temperature environments (Fig. 2). The interaction term, region × temperature, was only significant for RMR. Northern seedlings had significantly higher RMR than Southern seedlings at low temperature, but not at high temperature, reflected as a significant genotype × environment interaction (Table 2, Fig. 2). In the cold chamber the mean root investment of Northern families (RMR = 0.370) was greater than for that of Southern families (RMR = 0.334). In the hot chamber the means of Northern families (RMR = 0.265) was almost identical to that of Southern families (RMR = 0.270). An ANOVA using family means showed a significant regional effect in the cold chamber ($F = 10.1$, $P < 0.005$), but not in the hot treatment ($F = 0.0$, $P = 0.539$). In order to examine the genetic correlation between RMR in a hot environment and RMR in a cold environment within both regions, we calculated Pearson's correlation among least-squares family means (controlling for harvest date, Fig. 3) and computed 95% confidence intervals (CI) for the correlation between these two traits using a *z*-transformation (Sokal and Rolf 1995). For both regions the correlation of family means for RMR cold and RMR hot was significantly different from both zero and one. Southern and Northern families had correlation coefficients of 0.72 (95% CI = 0.33, 0.90) and 0.60 (95% CI = 0.13, 0.85), respectively.

### DISCUSSION

Our results show significant genetic variation between saltcedar families from both Montana and Arizona, the end points of the species' distributional range in the United States. Results also show significant plasticity for all functional traits sampled (morphological and gas exchange). Root biomass investments in cold and hot environments were found to be independent traits and thus can evolve independently (Falconer 1990). Although there were no genetic differences between regions for most traits, we found regional genetic divergence for root biomass investment in cold environments indicating ecotypic differentiation and perhaps local adaptation in seedlings. Overall, phenotypic plasticity, ecotypic differentiation and high genetic variation in saltcedar suggest that the invasive potential of this species is significant.

Consistent with generalized plant responses, gas exchange in saltcedar seedlings decreased significantly in response to decreasing temperatures (Berry and Raison 1981, Korner and Renhardt 1987, Friend and Woodward 1990); however, no genetic variation was detected. In a common garden study, Williams and Black (1993) also found no genetic differences in gas exchange as well as growth among populations of *Pennisetum setaceum*. They attribute the ability of this species to invade along a broad altitudinal range in Hawaii to phenotypic plasticity. Although our reduced sample size ($N = 82$ plants) for gas exchange traits reduced our ability to detect genetic variation, an analysis of
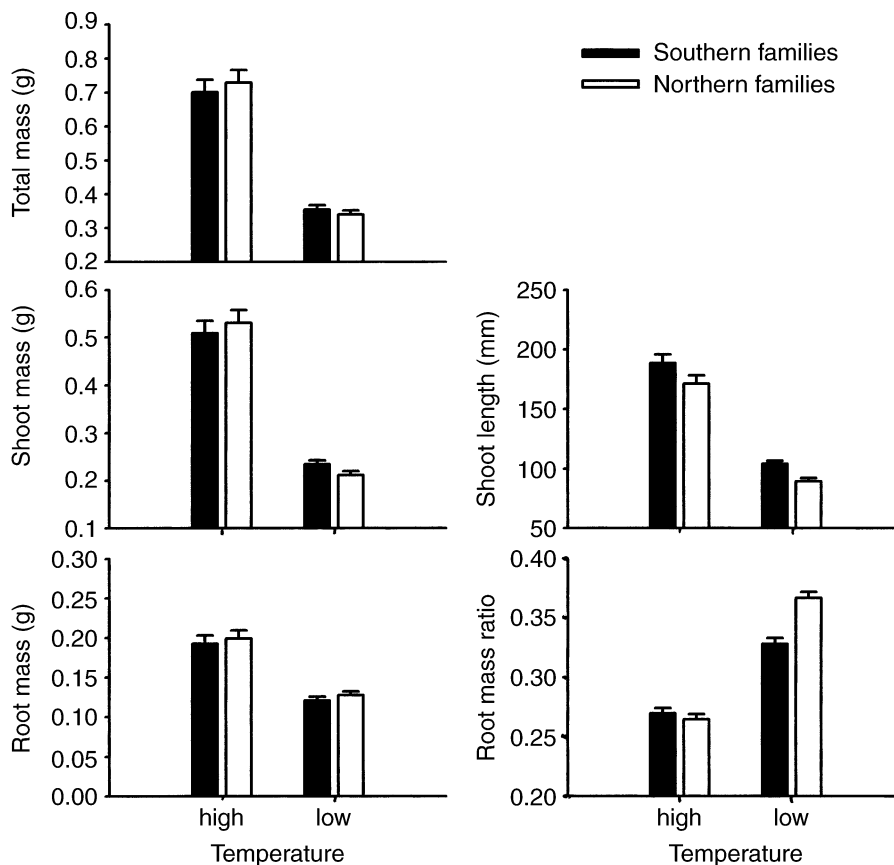
FIG. 2. Biomass allocation and growth in response to temperature for Southern (Arizona) and Northern (Montana) seedlings of *Tamarix ramosissima* grown in low-temperature (11°/25°C) and high-temperature (20°/37°C) environments. Shown are untransformed least-squares means for each region (controlling for harvest time) with vertical bars representing +1 SE. $N$ = 556 seedlings (278 for Southern, 278 for Northern) for root mass, total mass, and RMR; 559 (280 for Southern, 279 for Northern) for shoot mass; 530 (265 for Southern, 265 for Northern) for shoot length.

the same sample (blocks 2 and 10) revealed significant genetic variation between regions for shoot length. Thus we have good evidence for plasticity and no evidence for genetic variation in gas exchange traits, although we cannot rule out the possibility of undetected genetic variation.

The amount of genetic variation in non-native populations is affected by genetic drift (the number of introductions, founder population size, founder population diversity, and the breeding system of the invader) as well as selection in the novel habitat (Barrett 1982, Barrett and Richardson 1986, Bazzaz 1986, Novak and Mack 1993). The overall genetic variation in saltcedar's morphological traits was likely imported via multiple introductions from different regions in its native distribution, while geographic structure of the variation may be the result of recombination, intraspecific hybridization, drift, and/or selection since being introduced. This quantitative genetic variation is consistent with preliminary data showing significant variation in haplotypes in populations from the western U.S. (J. Gaskin, *personal communication*), suggesting a history

of multiple introductions. Montana's naturalized populations of saltcedar are thought to have escaped from plantings (for erosion control in irrigation developments) in central and northern Wyoming's Wind/Bighorn systems during the mid to late 1940s (C. Pearce, *personal communication*). Arizona's older, more invasive populations were spawned from ornamental and erosion control plantings from the late 1800s (Robinson 1965).

In general, cold temperature decreased plant height and increased RMR of saltcedar seedlings. In particular, Northern seedlings were shorter regardless of temperature and invested more in roots, but only when grown at low temperature (i.e., genotype × environment interaction for root investment). Heritable increases in belowground investment and plant dwarfism are common and have been related to decreased temperature, water, nutrients, and light (Chapin 1980, Ollerenshaw and Baker 1981, Wardlaw et al. 1983, Korner and Renhardt 1987, Friend and Woodward 1990). In cold climates, relative increased investment in roots allows increased belowground storage of reserves while min-
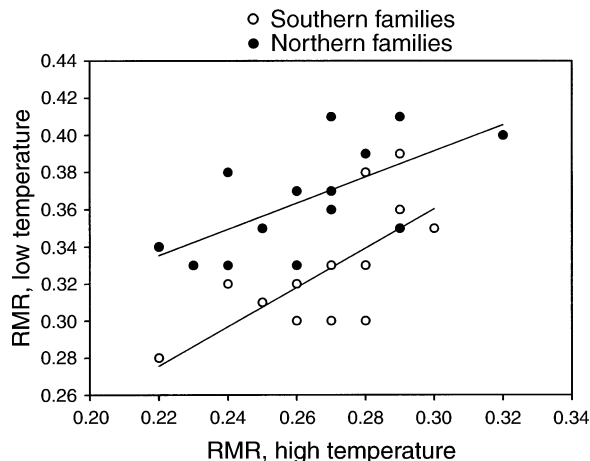
FIG. 3. Scatter plot of least-square family means (controlling for harvest time) for root mass ratio (RMR) in low-temperature vs. high-temperature chambers. Northern families (solid circles) have significantly higher RMR than Southern families (open circles) in the low-temperature chamber (*y*-axis). In the high-temperature chamber (*x*-axis) Northern families and Southern families were not significantly different, thus resulting in a significant region × temperature interaction (Table 2).

imizing heat transfer to the environment (Friend and Woodward 1990).

While seedling traits are clearly important for establishment, we know little about the contribution of recruitment to the intrinsic growth rate of introduced populations. Populations may also have genetically based differences in biomass allocation as adults. We did not analyze heritabilities or further partition genetic variance because we do not know whether our field collected families are full sibs, half sibs, or a mixture. Saltcedar has a self-compatible breeding system (Brotherson and Winkel 1986). The limitation of this experimental design is that we cannot statistically partition additive genetic variance from non-additive genetic variation due to dominance, epistasis, and maternal effects (Hiesey and Milner 1965). However, we removed environmental variance by blocking within families. Significant differences among families within each population suggest that differences between regions are not simply due to maternal effects resulting from large climatic differences between regions.

Controlled growth chamber screening allowed precise measurements during the seedling stage, particularly of relative biomass investment in roots, a fundamental trait during seedling establishment that would be very difficult to measure in the field. Although reciprocal transplants are necessary to test whether differences between regions have fitness consequences, we speculate that greater allocation of biomass to roots in response to cold may be adaptive for the Northern genotypes. If seeds from cold environments (Northern) germinate late in the season, underdeveloped seedlings may undergo high mortality during harsh winters. In-

creased relative allocation to roots in cold environments would minimize aboveground tissue losses due to freezing while maximizing resource storage in roots for subsequent growth during the generally shorter growing season. Small adjustments of root biomass can dramatically increase plant performance (Sultan 1992) and strong selection for increased root allocation may quickly affect future generations (Antonovics 1976). From a functional perspective, Northern populations may be experiencing selection for the greater root investment in the cold, or it may be possible that the amount of plasticity itself is responding to selection.

Under hot weather higher investment in aboveground structures would minimize shading by neighbors. In Northern and Southern regions, neighbor competition is particularly important if seeds germinate early in the growing season when native species also germinate (Everitt 1980). Rice et al. (1992) found that increases in shoot biomass in arid steppe populations of *Bromus tectorum* accelerated development and allowed life-cycle completion during opportune periods when soil moisture was available. Taken together, phenotypic plasticity, ecotypic differentiation, and substantial genetic variation may increase the potential of saltcedar to surpass the lag phase of the invasion process in the peripheries of its invasive range. If northern populations of saltcedar are experiencing selection (either for trait means or for phenotypic plasticity) their invasive potential could increase. The likelihood of adaptive genetic differentiation is increased if populations can persist in an area long enough to experience multiple episodes of natural selection (Barrett 1982). Indeed, saltcedar is persisting in northern, cold regions of the United States (J. Sexton, *personal observation*).

In light of this and other studies (see *Introduction*) we caution that levels of standing genetic variation in introduced species may greatly influence their future invasiveness, regardless of their current invasive status. If particular characters such as life history, competitive ability, and resistance to herbivores contribute to invasiveness, then any heritable variation in these characters can lead to evolutionary increases in invasiveness (Ellstrand and Schierenbeck 2000). Finally, the combined influences of founder effects and adaptive evolution following introduction join the list of explanations for the limited success of introducing natural enemies from the native range of invasive species as biological controls (Williamson and Fitter 1996b).

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