Native plant community composition and genetic diversity associated with long-term weed invasions

Brian A. Mealor  
*University of Wyoming, Laramie*

Ann L. Hild  
*University of Wyoming, Laramie*

Nancy L. Shaw  
*USDA Forest Service, Rocky Mountain Research Station, Boise, Idaho*

Follow this and additional works at: https://scholarsarchive.byu.edu/wnan

**Recommended Citation**


Available at: https://scholarsarchive.byu.edu/wnan/vol64/iss4/11

This Article is brought to you for free and open access by the Western North American Naturalist Publications at BYU ScholarsArchive. It has been accepted for inclusion in Western North American Naturalist by an authorized editor of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen amatangelo@byu.edu.
Exotic species often limit the ability of restoration ecologists to return native species to disturbed sites. Presence of exotic species may be a primary impetus for restoration activities. Exotics may become established following disturbances and often leave viable seed banks long after control efforts (D’Antonio and Meyerson 2002). Revegetation with competitive plants after chemical or mechanical treatments is needed to limit reestablishment of exotic invaders (Sheley and Stivers 1999, Whitson 1999). Because of the increasing demand for local native species in restoration, we must consider the genetic integrity of our native seed sources (Behnap 1995, Linhart 1995, Roundy et al. 1997, Jones and Johnson 1998). Yet it is unknown whether exotic invasions alter the genetic makeup of native plant populations by reducing native abundance. No study has considered the impact of long-term weed invasions on the genetic variability of remaining on-site native populations.

Restoration ecologists are concerned with constructing communities that are resistant to invasion by exotic species, even though our knowledge of invasive species ecology has not been well integrated into restoration and management (D’Antonio and Meyerson 2002). In this paper we unite invasive species ecology with restoration ecology in an effort to characterize interactions between native plants and their new exotic neighbors. This study describes a new approach for combating reentry of exotic weeds into restoration plantings.

Much literature suggests that invasion by exotic species may decrease native species diversity or alter nutrient cycles, thereby affecting community diversity (Elton 1958, Gordon 1998, Levine and D’Antonio 1999, Levine 2000). It is often assumed that exotics form monocultures and exclude native populations originally present on a site (Watson 1980). Even so, intrapopulation variability in native plants has been documented over very small distances (Linhart 1995, McGuinnies et al. 1998, Hild et al. 1999) and over short time periods (Snaydon and Davies 1982, Al-Hiyaly et al. 1988, 1989). Linhart and Grant (1996) assert that “genetic differentiation could be observed over distances of even a few meters, and, whenever localized selection was sufficiently intense, even a few centimeters.” These studies investigated local differentiation of native plant populations in response to changing environmental conditions, but not to the presence of exotic weeds. We examine differences in native plant populations within weed invasions and in adjacent, noninvaded areas. We
Ask if long-term coexistence with exotic neighbors may, over time, select for a unique subset of native plant genotypes.

Invasive species can increase in competitive ability (Blossey and Notzold 1995), grow larger (Siemann and Rogers 2001), hybridize (Ellstrand and Schierenbeck 2000), and even change their modes of reproduction (Amsellem et al. 2001) after introduction into new ranges. This suggests that new environmental conditions (including interactions with neighboring natives) can shape an exotic species over time (Mooney and Cleland 2001). However, no evidence has documented changes in native plant populations after exposure to an exotic. Our studies focus upon the influence of invading species on the genetic diversity of native plant populations. We suggest that the inherent variability within native populations may allow for their perpetuation via competitive selection by exotic neighbors. Given sufficient time, exotic neighbors may select for native populations that exhibit combining ability (Harper 1977, Aarssen 1983, Aarssen and Turkington 1985, Goodwin et al. 1999, Callaway and Aschehoug 2000).

To test these ideas, we examined species presence and abundance in old (>25 years) sites invaded by *Acroptilon repens* L. (*Centaurea repens*, Russian knapweed) and *Cardaria draba* L. (Desv.) (*Lepidium draba* L. DC., hoary cress, whitetop) in Wyoming and Idaho. We document species richness and abundance of natives in old invasions of *Acroptilon* and *Cardaria* to examine the hypothesis that native species may remain in invasions in small numbers as resistant, remnant individuals. Then we use an anonymous genetic fingerprint analysis to determine if genotypic characteristics of natives from within differ from those of individuals immediately outside the invasion.

**Materials and Methods**

In spring 2001 we contacted county weed and pest agents, landowners, and federal agency staff to find extensive invasions of *Acroptilon repens* and *Cardaria draba* in Wyoming and Idaho. We selected these 2 weed species because they are highly competitive perennial plants that are widely dispersed throughout the Intermountain West and are reported to form dense, monospecific stands (Watson 1980, Sheley and Stivers 1999).

We assessed more than 20 potential field sites, evaluating them for age of invasion, size of the invaded area (>25 m²), lack of cultivation history, and presence of nearby noninvaded native community. We selected 4 replicate sites for each weed species in Wyoming and Idaho (Table 1). The Greybull, Wyoming, field site was included in the analysis for both *Acrop-tilon* and *Cardaria* because both exotics were present at high densities. All field locations were in severe drought during 2001 and 2002 (NOAA 2003).

In 2001 and 2002, to distinguish invaded from noninvaded positions at each field site, we sampled exotic weed densities in 0.25-m² rectangular quadrats along 2 parallel transects (Fig. 1). Areas with high densities of *Acroptilon repens* or *Cardaria draba* were considered

<table>
<thead>
<tr>
<th>Exotic species</th>
<th>Site</th>
<th>Elevation (m)</th>
<th>Annual precipitation (cm)</th>
<th>Mean temperature (°C)</th>
<th>Age of invasion (years)</th>
<th>Exotic density (stems · m⁻²)</th>
<th>Soil texture</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cardaria draba</em></td>
<td>Bancroft, ID</td>
<td>1740</td>
<td>38</td>
<td>6.9</td>
<td>25</td>
<td>276</td>
<td>silt loam</td>
</tr>
<tr>
<td></td>
<td>Dubois, WY</td>
<td>2210</td>
<td>24</td>
<td>5.0</td>
<td>25</td>
<td>45</td>
<td>loamy sand</td>
</tr>
<tr>
<td></td>
<td>Greybull, WY</td>
<td>1190</td>
<td>18</td>
<td>7.1</td>
<td>35</td>
<td>57</td>
<td>silty clay</td>
</tr>
<tr>
<td></td>
<td>Rock Springs, WY</td>
<td>2010</td>
<td>23</td>
<td>6.0</td>
<td>30</td>
<td>201</td>
<td>silty clay loam</td>
</tr>
<tr>
<td><em>Centaurea repens</em></td>
<td>Greybull, WY</td>
<td>1190</td>
<td>18</td>
<td>7.1</td>
<td>35</td>
<td>51</td>
<td>silty clay</td>
</tr>
<tr>
<td></td>
<td>Mud Lake, ID</td>
<td>1460</td>
<td>21</td>
<td>6.7</td>
<td>30</td>
<td>80</td>
<td>loamy sand</td>
</tr>
<tr>
<td></td>
<td>Rogerson, ID</td>
<td>1520</td>
<td>27</td>
<td>8.8</td>
<td>90</td>
<td>20</td>
<td>loam</td>
</tr>
<tr>
<td></td>
<td>Rock Springs, WY</td>
<td>2000</td>
<td>23</td>
<td>6.0</td>
<td>30</td>
<td>35</td>
<td>sandy clay loam</td>
</tr>
</tbody>
</table>

*aAge of invasion was based on observations of local landowners and managers.*
invaded, and areas with no target exotics that were located within 20 m of high weed densities were considered noninvaded. In several instances noninvaded areas contained sporadic individuals of exotic plants (<1 m²). In each of 2 positions (invaded, noninvaded) we defined 25-m² sampling areas separated by <20 m sharing the same slope, aspect, and soil properties. Within each sampling area we established five 1-m² quadrats and counted grass culm and weed stem densities within each quadrat. Species richness was compiled over the entire 25-m² sampling area, combining the 2001 and 2002 growing season samples.

To evaluate whether native diversity and abundance were reduced inside invasions, we documented native and total species density (culms · m⁻²), species richness, and diversity (H'; Shannon and Weaver 1949) at each site. Richness and diversity of the 2 positions (treatments) and 4 field sites (replicates) were compared within each weed species using Student's paired t-test statistic (SAS Institute 1999).

**Native Plant Population Genotypic Variation in the Two Positions**

To characterize the genetic makeup of native plant populations within the 2 positions, we sampled native plant foliage for anonymous genetic fingerprinting. From the same study sites, we collected plant foliage from *Poa secunda* Presl., *Hesperostipa comata* Roem. and Schult., and *Sporobolus airoides* from *Acrop-tilon* invasions and *Achnatherum hymenoides* (Trin. and Rupr.) Barkworth and *Sporobolus airoides* from *Cardaria* invasions. These native grasses represent a range of reproductive modes from primarily inbreeding to obligate outcrossers. *Sporobolus airoides* is self-pollinating and *Achnatherum hymenoides* is considered mostly selfing (Jones and Nielson 1989), while *Hesperostipa comata* and *Poa secunda* are mixed pollinators (Fryxell 1957, Larson et al. 2001). Drought conditions restricted the native species available for genetic analysis because many plants had senesced very early in the growing season. Foliage samples were collected between 28 May and 6 June 2002. After collection, samples were placed in silica gel, stored in a cooler during transport, and frozen to −20°C until DNA extraction. Only fresh, actively photosynthesizing leaf material was collected for inter-simple sequence repeat (ISSR) analysis.

**ISSR analysis** is a procedure used to assess genetic variation in plants by presence or absence of recognizable bands of DNA fragments (Deshpande et al. 2001, Stenstrom et al. 2001, Tuthill and Brown 2003). ISSR markers are based on microsatellite loci initially developed by Zietkiewicz et al. (1994) and Gupta et al. (1994). Primers are designed to match
segments of tandemly repeated bases (e.g., TCTCTC, a microsatellite) with extra base pairs of randomly chosen sequence on the end, called “anchors.” These primers are used singly in polymerase chain reactions (PCR) and attach only where there is a matching microsatellite locus and adjacent sequence matching the anchor. The PCR reactions amplify segments between microsatellites to produce multiple banding patterns that have been used for genomic fingerprinting, differentiation between crop cultivars, exploring population structure (Zhou et al. 1999, Deshpande et al. 2001, Tuthill and Brown 2003), elucidating phylogenetic relationships (Wolfe et al. 1998), constructing genomic maps, and documenting interspecific hybridization (Wolfe and Liston 1998). ISSR methods also show great promise as a method of examining relationships among individuals within populations and between populations (Meekins et al. 2001). ISSR primers used in this study are listed in Table 2.

DNA was extracted from leaves using standard 2X CTAB protocol (Doyle and Doyle 1987). The 20-µL PCR reactions consisted of 1X buffer (Sigma; 10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.5 M MgCl2, 0.0001% gelatin), additional 50 mmol MgCl2, 8 nmol dNTPs, 6 nmol primer, 10 µg BSA, 3 µL saturated betaine, 1 unit Taq polymerase, and 1 µL DNA. Thermal cycling parameters were initial denaturing for 2 minutes at 96°C, followed by 40 cycles of 30 seconds at 96°C, 45 seconds at 44°C, and 90 seconds at 72°C, with a final elongation at 72°C for 10 minutes. PCR reactions were visualized following electrophoresis on 1.5% agarose gels stained with ethidium bromide at a standard time of 75 minutes. We used a Bio-Rad Versadoc system to take direct digital photos of the gels. Gels were scored directly from digital photos for presence (1) or absence (0) of obvious, repeatable bands (present in 2 separate runs). We used 9 primers that produced from 36 to 118 scorable, informative bands for each species.

Banding patterns were used to calculate percent polymorphic loci (P) and genetic diversity within populations (Hs) for each position. We calculated coefficient of population differentiation (Gst) and Nei’s unbiased genetic distance (D) to compare positions. All genetic statistics were calculated using Popgen32 (Yeh et al. 1997) and treating positions as populations. A locus was designated polymorphic if it contained 2 or more alleles within a population. The percentage of polymorphic loci (P) within a population provides a measure of genetic variability. Heterozygosity within populations (Hs) is a measure of genetic variation that is useful for genes of different ploidy levels and in different organisms with different reproductive systems (Nei 1987). This measure is more applicable for comparing across species that differ reproductively, as do our species. The coefficient of population differentiation

<table>
<thead>
<tr>
<th>Primer</th>
<th>Sequence</th>
<th>ACHY</th>
<th>HECO</th>
<th>POSE</th>
<th>SPAI</th>
</tr>
</thead>
<tbody>
<tr>
<td>807</td>
<td>AG_A_7</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>813</td>
<td>CT_A_7</td>
<td>Fair</td>
<td>Fair</td>
<td>Fair</td>
<td>Fair</td>
</tr>
<tr>
<td>815</td>
<td>CT_A_7</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>823</td>
<td>CT_G_7</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>834</td>
<td>AG_A_CT_7</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>836</td>
<td>AG_A_CT_7</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>846</td>
<td>CA_A_GT_7</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>848</td>
<td>CA_A_GG_7</td>
<td>Good</td>
<td>n/a</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>857</td>
<td>AC_A_CT_7</td>
<td>Good</td>
<td>n/a</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>868</td>
<td>GA_A_GT_7</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>873</td>
<td>GACA_4</td>
<td>Good</td>
<td>Good</td>
<td>n/a</td>
<td>Good</td>
</tr>
<tr>
<td>881</td>
<td>GGGT_GGGT_2G</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
<td>Good</td>
</tr>
<tr>
<td>891</td>
<td>ACTACGACT(TG)_7</td>
<td>Fair</td>
<td>Fair</td>
<td>Fair</td>
<td>Fair</td>
</tr>
<tr>
<td>894</td>
<td>TGGTAGCTCTTGATCA(ACTG)_5</td>
<td>n/a</td>
<td>Poor</td>
<td>n/a</td>
<td>Poor</td>
</tr>
</tbody>
</table>

*Primer sequences (oriented 5' → 3'), letters within parentheses represent the tandemly repeated segment of the primer. Values of primers (good, fair, poor) were based on quality, quantity, and repeatability of band production within a species. If a primer was not used on a species, it is valued as n/a.
(G_{st}) measures the amount of total gene diversity attributed to differences between positions. Nei’s unbiased genetic distance (D) is a statistical measure that provides a standardized scale for the quantification of genetic differences (Hoelzel and Dover 1991).

To better understand patterns of variation within and between populations, we performed unweighted pair-group mean analysis (UPGMA) on matrices of similarity calculated from all possible pairwise combinations of individuals using Dice’s (1945) coefficient of similarity (NTSYS-pc; Rohlf 1989). We ran 1000 bootstrap searches for each dendrogram to include confidence intervals. Dice’s coefficient emphasizes shared traits (ISSR fragments in this study) among individuals and ignores shared trait absence.

### RESULTS

#### Field Study

Interestingly, species richness, native species diversity, and total species diversity did not differ between the 2 positions (invaded and noninvaded) across the 4 replicate sites for either exotic species ($P > 0.05$), even though the exotics had been on site for ≥25 years (Table 3). However, abundance (culm density) of *Hesperostipa comata* did not differ between positions for either exotic species.

### Table 3. Plant species richness and diversity ($H’$) in invaded and noninvaded positions in four sites for each weed species.

<table>
<thead>
<tr>
<th>Exotic species</th>
<th>Site Position</th>
<th>Native richness</th>
<th>Native diversity</th>
<th>Total richness</th>
<th>Total diversity</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Cardaria draba</em></td>
<td>Bancroft, ID</td>
<td>Invaded</td>
<td>7</td>
<td>0.08</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Noninvaded</td>
<td>4</td>
<td>0.06</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Dubois, WY</td>
<td>Invaded</td>
<td>9</td>
<td>0.46</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Noninvaded</td>
<td>11</td>
<td>0.65</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Greybull, WY</td>
<td>Invaded</td>
<td>5</td>
<td>0.49</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Noninvaded</td>
<td>10</td>
<td>0.30</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Rock Springs, WY</td>
<td>Invaded</td>
<td>10</td>
<td>0.25</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Noninvaded</td>
<td>12</td>
<td>0.54</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>Mean ± s.d</td>
<td>Invaded</td>
<td>6.3 ± 0.88</td>
<td>0.38 ± 0.05</td>
<td>11.0 ± 1.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Noninvaded</td>
<td>7.7 ± 1.23</td>
<td>0.34 ± 0.06</td>
<td>8.9 ± 1.07</td>
</tr>
</tbody>
</table>

| Acroptilon repens | Greybull, WY | Invaded | 5 | 0.49 | 9 | 0.59 |
| | | Noninvaded | 10 | 0.30 | 14 | 0.44 |
| | Mud Lake, ID | Invaded | 11 | 0.30 | 14 | 0.44 |
| | | Noninvaded | 12 | 0.35 | 14 | 0.61 |
| | Rogerson, ID | Invaded | 3 | 0.08 | 6 | 0.49 |
| | | noninvaded | 5 | 0.19 | 6 | 0.41 |
| | Rock Springs, WY | Invaded | 10 | 0.63 | 14 | 0.59 |
| | | Noninvaded | 12 | 0.56 | 18 | 0.66 |
| | Mean ± s.d | Invaded | 6.4 ± 0.95 | 0.33 ± 0.07 | 10.1 ± 0.91 | 0.52 ± 0.04 |
| | | Noninvaded | 7.0 ± 0.62 | 0.35 ± 0.08 | 9.7 ± 0.71 | 0.55 ± 0.05 |
Genetic Variation
Within Positions

Polymorphism in the *Sporobolus* populations was reduced in the invaded position ($P = 47.6\%$; Table 4) relative to the noninvaded position ($P = 69.1\%$; Table 4). The remaining native species were more polymorphic in invaded than in noninvaded positions. Mean heterozygosity for all populations studied was 0.223, and $H_S$ values varied among the 4 species, the most obvious difference in heterozygosity being observed in *Hesperostipa comata*.

Genetic Variation
Between Positions

For each species examined, the greatest portion of variation was within positions. For example, for *Sporobolus*, the $G_{st}$ (0.121) indicates that the proportion of genetic diversity between positions contributed 12.1\% of the total genetic diversity in the individuals we sampled. *Hesperostipa*, *Achnatherum*, and *Poa* varied more between positions than did *Sporobolus* (Table 4). The greatest genetic distance was observed between *Poa secunda* positions ($D = 0.446$; Table 4), and $D$ varied according to species. *Sporobolus airoides* differed least ($D = 0.122$) between positions of the 4 species sampled.

The UPGMA cluster analysis revealed interesting patterns specific to each species. Individuals of *Hesperostipa comata* were separated into 2 distinct, yet fairly similar (0.74), clusters according to position (Fig. 2). *Sporobolus airoides* individuals were more intermixed by position, but still clustered within positions (Fig. 3). *Poa secunda* and *Achnatherum hymenoides* individuals were less similar overall. *Poa* individuals were clustered with no apparent pattern (Fig. 4), while *Achnatherum* individuals formed 3 fairly distinct clusters, 2 of which seemed to separate by position (Fig. 5).

DISCUSSION

Contrary to popular views of invasions (sensu monospecific stands), our results demonstrate that native species remain within weed invasions (although in reduced abundance). Perhaps *Acroptilon repens* and *Cardaria draba* do not change ecosystem attributes enough to exclude native species. However, it is important to note that our field sites had no history of cultivation and may have lacked sufficient disturbance of the native community to result in monospecific stands.

There were no clear correlations between breeding system and genetic variability. Differences in $H_S$ are more subtle but follow the same pattern as the polymorphism results.

When comparing the 4 species, our $G_{st}$ results are mixed. While 3 of 4 species have relatively high portions of variability attributed to positions, they do not follow modes of
Fig. 2. UPGMA cluster analysis using Dice’s coefficient of similarity (NTSYS-pc) of individual native grass plants of *Hesperostipa comata* from an *Acroptilon* invasion near Mud Lake, ID. Dendrogram is based on presence and absence of ISSR bands within plants derived from the 2 positions (invaded ■, noninvaded ●) relative to exotics. Bootstrap confidence levels are indicated for clusters present in the 50% majority-rule consensus of 1000 UPGMA searches.

Fig. 3. UPGMA cluster analysis using Dice’s coefficient of similarity (NTSYS-pc) of individual native grass plants of *Sporobolus airoides* from an *Acroptilon* and *Cardaria* mixed invasion near Greybull, WY. Dendrogram is based on presence and absence of ISSR bands within plants derived from the 2 positions (invaded ■, noninvaded ●) relative to exotics. Bootstrap confidence levels are indicated for clusters present in the 50% majority-rule consensus of 1000 UPGMA searches.
Fig. 4. UPGMA cluster analysis using Dice’s coefficient of similarity (NTSYS-pc) of individual native grass plants of *Poa secunda* from an *Acroptilon* invasion near Rock Springs, WY. Dendrogram is based on presence and absence of ISSR bands within plants derived from the 2 positions (invaded ■, noninvaded ●) relative to exotics. Bootstrap confidence levels are indicated for clusters present in the 50% majority-rule consensus of 1000 UPGMA searches.

Fig. 5. UPGMA cluster analysis using Dice’s coefficient of similarity (NTSYS-pc) of individual native grass plants of *Achnatherum hymenoides* from a *Cardaria* invasion near Dubois, WY. Dendrogram is based on presence and absence of ISSR bands within plants derived from the 2 positions (invaded ■, noninvaded ●) relative to exotics. Bootstrap confidence levels are indicated for clusters present in the 50% majority-rule consensus of 1000 UPGMA searches.
reproduction. For example, *Sporobolus airoides* is a self-pollinator but has the lowest value (this may be attributed to the longevity of the species). Genetic distance (D) results for *Sporobolus* are comparable to $G_{st}$, and no clear pattern emerges among the 4 species. However, both D and $G_{st}$ results demonstrate that there are differences between the 2 positions within each species.

Our collections within species are limited to individuals from single sites, a restriction that may be important for finding differences at the neighborhood scale (sensu Aarssen 1983). Had we included additional control populations spatially separated from those we sampled, we could have addressed genetic differences due to spatial separation alone. There is little information available on the genetic variability of native grasses within local populations, and subsequent study is currently underway to document such patterns.

Our genetic data suggest that population differentiation is occurring within weed invasions. Divergence in our populations may not be solely attributed to prolonged coexistence with exotic species. Such differentiation could result from founder effects and genetic drift in addition to natural selection within exotic invasions. Given the complexity of natural systems, it is likely that multiple mechanisms of evolution come into play. Reduced abundance of some natives within invasions indicates population bottlenecks. It is difficult to discern between neutral forces (i.e., founder effects, drift) and selection in a study such as this. Future study is required to assess whether the genetic differences we observed translate into biologically meaningful advantage against exotics. The separation of selection from neutral forces should be addressed and suggests an important avenue of research. Consequently, we cannot say that the genetic differences we noted are the results of selection for greater competitive ability with weeds. Because we do not know the longevity of these species, it is possible that natives may have simply persisted within the invasions. Even so, such relict native individuals would have been subject to the novel selective environment of the weed invasion. If *Acerptilion repens* and *Cardaria draba* have altered the growing conditions on our sites, they could have facilitated divergence in the native populations through selection, rather than neutral forces, in a short time (Whitlock 1997). We know that exotic plant invasions can drastically alter the environment in which they occur (Gordon 1998). Subsequent study is needed to ascertain the probable sources of the genetic differences we observed and to document adaptive traits in native grass populations that may contribute to native success against weed invasions.

Our genetic data (Fig. 2, Table 4) parallel other studies of population differentiation and microdifferentiation in natural populations (Thompson 1999, Gitzendanner and Soltis 2000, Deshpande et al. 2001). Differentiation between positions for *Poa secunda* ($G_{st}$) is high when compared with previous studies (Larson et al. 2001), but we sampled fewer individuals from each position, which may have elevated this statistic in our results. Our sampling was negatively affected by drought throughout the study, and increased sample sizes would have been preferred.

We began by asking if native plant individuals remain on sites after long-term invasion by exotics. They did in our study, although in reduced abundance. We next asked if con specifics differed between invaded and noninvaded areas. The genotypic differences observed in the native species we sampled suggest that native communities may have the ability to respond to exotic invasion. Native species richness and diversity were not significantly different in invaded areas even though each exotic species of interest was the dominant species in that community.

Our results represent an initial attempt to document intraspecific genetic variation of native species in old weed invasions, which may hold important implications for restoration ecology. There are many approaches to examine suitable species sources for restoration (Linhart 1995, Roundy et al. 1997, Jones and Johnson 1998), but few studies examine native genotypic variability associated with invasive exotics. There is a lack of evidence documenting local-scale ties of intraspecific diversity to ecosystem function (Belnap 1995, Linhart 1995, Madritch and Hunter 2002, Partel 2002).

Because competitive, or tolerant, native genotypes may be developing with prolonged exposure to exotic neighbors, we suggest that knowledge of post-invasion native plant population dynamics is critical to returning ecosystem function following exotic plant invasions. Community invasibility may be affected by
resource fluctuation (Davis et al. 2000), increased competitive ability (Blossey and Notzold 1995), and diversity (Levine and D’Antonio 1999). Remnant native genotypes may be the basis of community resistance, and mechanisms leading to native species coexistence with invasive exotics should be investigated more completely. Thus far, research on native populations’ response to invasion has been overlooked.

Finally, we have not documented competitive success of our native populations. Both exotic species are best controlled by revegetation with competitive grasses following chemical or mechanical control methods (Bottoms and Whitson 1998, Sheley and Stivers 1999, Whitson 1999). Future greenhouse and field studies will allow us to document relative competitive abilities of natives from invaded areas and to identify traits that may contribute to competitive success against exotic weeds. Such research efforts examining intraspecific genotypes may identify a promising opportunity for revegetation following weed control.

ACKNOWLEDGMENTS

We thank the many landowners and managers who cooperated on this project, D.E. Tuthill and G.K. Brown for genetic laboratory facilities and assistance, and D. Kazmer and S. Miller for early input on this project. This work was supported by USDA-NRI Seed Grant 2001-35311-09846. We appreciate the field assistance provided by students in the University of Wyoming Shrubland Ecology Lab and the staff at the Rocky Mountain Research Station. Special thanks to C.L. Kinter, R.K. Peet, E.D. McArthur, and several anonymous reviewers for reading earlier versions of this manuscript.

LITERATURE CITED


ecotones. USDA, Forest Service Proceedings RMRS P-11, Ogden, UT.


Received 16 July 2003
Accepted 13 April 2004