Western North American Naturalist 64(4), © 2004, pp. 503–513

NATIVE PLANT COMMUNITY COMPOSITION AND GENETIC DIVERSITY ASSOCIATED WITH LONG-TERM WEED INVASIONS

Brian A. Mealor[1], Ann L. Hild[1], and Nancy L. Shaw[2]

ABSTRACT.—Many studies have assessed genetic changes in exotic plant species in their native and introduced ranges, but none have focused on genetic variation in native plant species in response to exotic invasion. We examine characteristics of native plant communities within and outside old (>25 year) invasions of *Acroptilon repens* (Russian knapweed) and *Cardaria draba* (hoary cress). We also document genetic variability of 4 native grass populations (*Hesperostipa comata* [needle and thread], *Achnatherum hymenoides* [Indian ricegrass], *Sporobolus airoides* [alkali sacaton], and *Poa secunda* [Sandberg bluegrass]) from 2 areas: adjacent to and within weed invasions. Native plant species richness and diversity did not differ between invaded and noninvaded areas. Inter-simple sequence repeat (ISSR) analysis of individual native perennial grasses of each of the 4 species suggests that populations exposed to long-term coexistence with exotics may differ from adjacent noninvaded populations. We suggest that future research efforts should focus on intraspecific diversity of native plant species to identify possible candidates for restoration following weed control.

Key words: native grasses, invasive plants, diversity, ISSR, Acroptilon repens, Cardaria draba, Achnatherum hymenoides, Hesperostipa comata, Sporobolus airoides, Poa secunda.

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 (Belnap 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

[1]Department of Renewable Resources, University of Wyoming, Box 3354, Laramie, WY 82071-3354.
[2]USDA Forest Service, Rocky Mountain Research Station, 344 E. Front St., Boise, ID 83702.

TABLE 1. Descriptive characteristics of 4 study sites invaded either by *Acroptilon repens* or *Cardaria draba* in Wyoming and Idaho

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

[a]Age of invasion was based on observations of local landowners and managers.

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 (Amsellam 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 m^2), 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 *Acroptilon* 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-m^2 rectangular quadrats along 2 parallel transects (Fig. 1). Areas with high densities of *Acroptilon repens* or *Cardaria draba* were considered

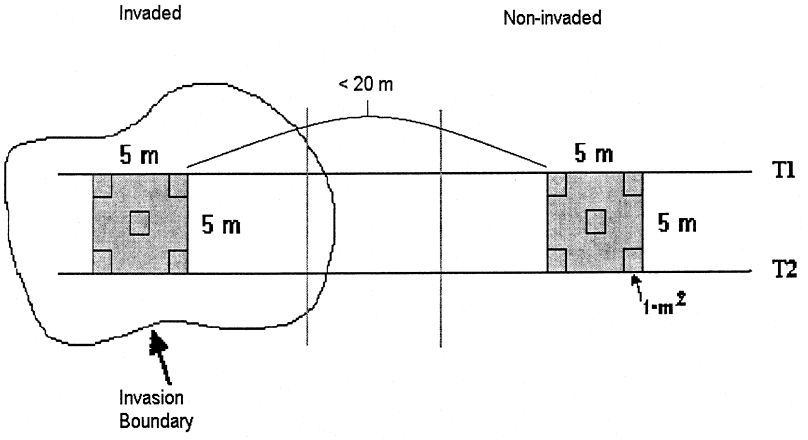

Fig. 1. Field sampling layout at all field locations. Target exotic plant densities were determined in 0.25-m^2 quadrats along 2 parallel transects (T1, T2) to distinguish invaded from noninvaded positions. Species richness was recorded, and seed and leaf tissue samples were collected within the large 25-m^2 areas. Individual species abundance was determined in five 1-m^2 plots within each position. Sampling plots were separated by no more than 20 m.

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 m^2). In each of 2 positions (invaded, noninvaded) we defined 25-m^2 sampling areas separated by <20 m sharing the same slope, aspect, and soil properties. Within each sampling area we established five 1-m^2 quadrats and counted grass culm and weed stem densities within each quadrat. Species richness was compiled over the entire 25-m^2 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 $\cdot$ 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 *Acroptilon* 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

TABLE 2. Summary of ISSR primers used to assess genetic variation in 4 native grass species (ACHY = *Achnatherum hymenoides,* HECO = *Hesperostipa comata*, POSE = *Poa secunda,* and SPAI = *Sporobolus airoides*).

Primer[a]	Sequence	ACHY	HECO	POSE	SPAI
807	$(AG)_8T$	Good	Good	Good	Good
813	$(CT)_8T$	Fair	Fair	Fair	Fair
815	$(CT)_8G$	Good	Good	Good	Good
823	$(TC)_8C$	Good	Good	Good	Good
834	$(AG)_8CTT$	Good	Good	Good	Good
836	$(AG)_8CTA$	Good	n/a	n/a	n/a
846	$(CA)_8AGT$	n/a	n/a	n/a	Good
848	$(CA)_8AGG$	Good	n/a	n/a	n/a
857	$(AC)_8CTG$	Good	n/a	Good	Good
868	$(GAA)_6$	Good	Good	Good	Good
873	$(GACA)_4$	Good	Good	n/a	Good
881	GGGT(GGGGT)2G	Good	Good	Good	Good
891	$ACTACGACT(TG)_7$	Fair	Fair	Fair	Fair
894	$TGGTAGCTCTTGATCA(ACTG)_5$	n/a	Poor	n/a	Poor

[a]Primers were provided by the University of British Columbia, Nucleic Acid Service-Protein Unit. In the 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.

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 $MgCl_2$, 0.0001% gelatin), additional 50 nmol $MgCl_2$, 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 (H_s) for each position. We calculated coefficient of population differentiation (G_{st}) 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 (H_s) 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 3. Plant species richness and diversity (H′) in invaded and noninvaded positions in four sites for each weed species.

Exotic species Site Position	Native richness	Native diversity	Total richness	Total diversity
Cardaria draba				
Bancroft, ID				
Invaded	7	0.08	13	0.55
Noninvaded	4	0.06	11	0.35
Dubois, WY				
Invaded	9	0.46	13	0.52
Noninvaded	11	0.65	14	0.75
Greybull, WY				
Invaded	5	0.49	9	0.59
Noninvaded	10	0.30	14	0.44
Rock Springs, WY				
Invaded	10	0.25	13	0.73
Noninvaded	12	0.54	19	0.42
Mean ± $s_{\bar{x}}$				
Invaded	6.3 ± 0.88	0.38 ± 0.05	11.0 ± 1.2	0.45 ± 0.03
Noninvaded	7.7 ± 1.22	0.34 ± 0.06	8.8 ± 1.07	0.51 ± 0.05
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 ± $s_{\bar{x}}$				
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

(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 *Achnatherum hymenoides* ($t_{1,3} = -5.14$, $P = 0.007$), *Poa secunda* ($t_{1,3} = 3.12$, $P = 0.035$), and *Sporobolus airoides* ($t_{1,3} = 6.34$, $P = 0.003$) was greater outside invasions of both exotic species. Abundance of *Hesperostipa comata* did not differ between positions for either exotic species.

TABLE 4. Genetic statistics ([a]P, H_s, G_{st}, and D) of 4 grass species derived from invaded and noninvaded positions. Coefficient of population differentiation (G_{st}) and Nei's unbiased genetic distance (D) were calculated treating positions as populations, hence the genetic distance values report between positions at each site.

Species Position	P	H_s	G_{st}	D
Hesperostipa comata				
Invaded (n = 10)	55.3	0.203	0.353	0.257
Noninvaded (n = 10)	46.8	0.156		
Sporobolus airoides				
Invaded (n = 6)	47.6	0.203	0.121	0.122
Noninvaded (n = 6)	69.1	0.259		
Poa secunda				
Invaded (n = 3)	51.4	0.230	0.324	0.446
Noninvaded (n = 3)	48.6	0.252		
Achnatherum hymenoides				
Invaded (n = 5)	61.0	0.243	0.303	0.276
Noninvaded (n = 5)	60.2	0.234		

[a]Percentage polymorphism (P); heterozygosity within population (H_s); coefficient of population differentiation (G_{st}); Nei's unbiased genetic distance between populations (D).

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 interspersed 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

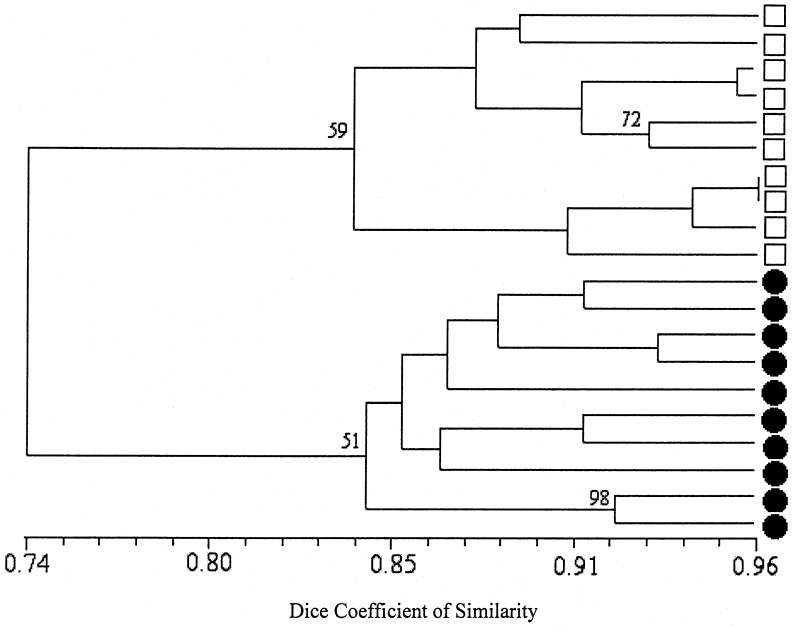

Fig. 2. UPGMA cluster analysis using Dice's coefficient of similarity (NTSYS-pc) of individual native grass plants of *Hesperostipa comata* from an *Acroptilon* invasion near Mud Lake, ID. Dendrogram is based on presence and absence of ISSR bands within plants derived from the 2 positions (invaded □, noninvaded ●) relative to exotics. Bootstrap confidence levels are indicated for clusters present in the 50% majority-rule consensus of 1000 UPGMA searches.

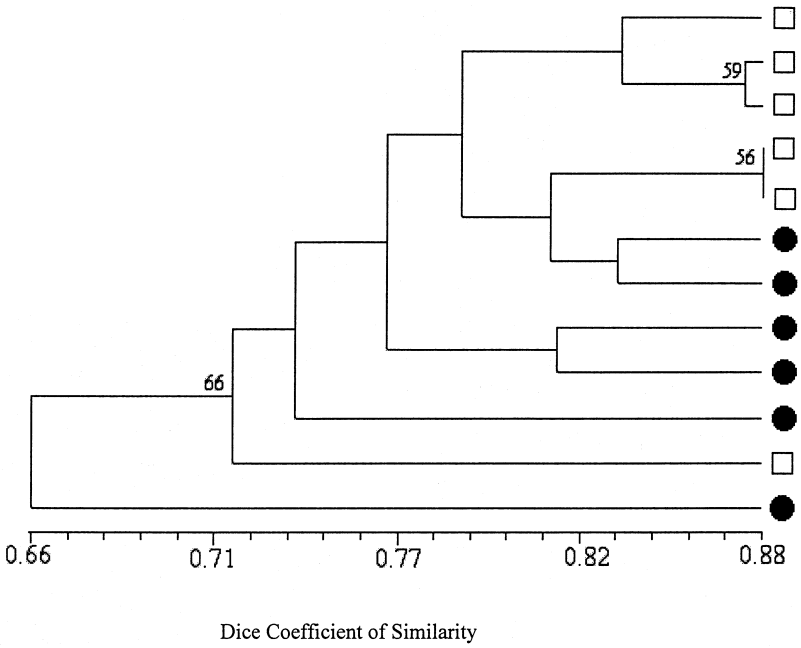

Fig. 3. UPGMA cluster analysis using Dice's coefficient of similarity (NTSYS-pc) of individual native grass plants of *Sporobolus airoides* from an *Acroptilon* and *Cardaria* mixed invasion near Greybull, WY. Dendrogram is based on presence and absence of ISSR bands within plants derived from the 2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

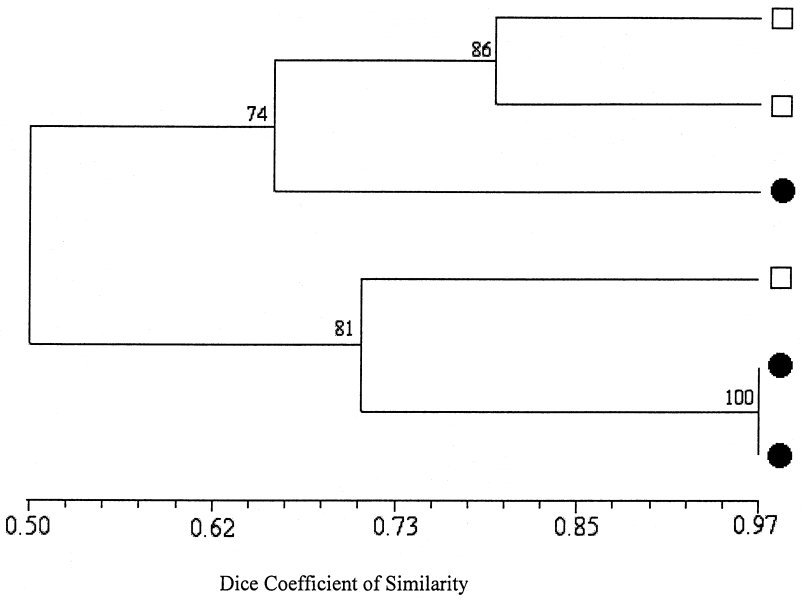

Fig. 4. UPGMA cluster analysis using Dice's coefficient of similarity (NTSYS-pc) of individual native grass plants of *Poa secunda* from an *Acroptilon* invasion near Rock Springs, WY. Dendrogram is based on presence and absence of ISSR bands within plants derived from the 2 positions (invaded □, noninvaded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

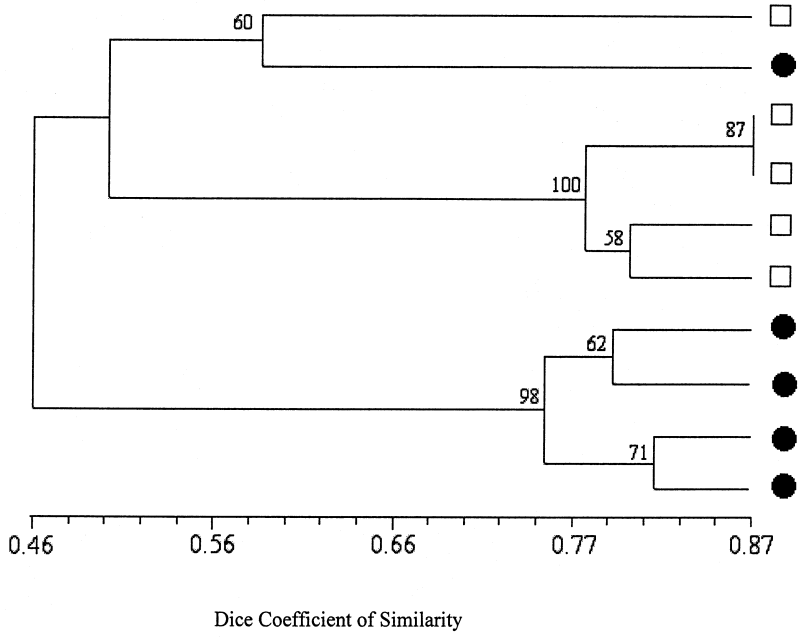

Fig. 5. UPGMA cluster analysis using Dice's coefficient of similarity (NTSYS-pc) of individual native grass plants of *Achnatherum hymenoides* from a *Cardaria* invasion near Dubois, WY. Dendrogram is based on presence and absence of ISSR bands within plants derived from the 2 positions (invaded □, noninvaded ●) 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 *Acroptilon 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 conspecifics 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

AARSSEN, L.W. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. American Naturalist 122:707–731.

AARSSEN, L.W., AND R. TURKINGTON. 1985. Competitive relations among species from pastures of different ages. Canadian Journal of Botany 63:2319–2325.

AL-HIYALY, S.A.K., T. MCNEILLY, AND A.D. BRADSHAW. 1988. The effects of zinc contamination from electricity pylons: evolution in a replicated situation. New Phytologist 110:571–580.

_____. 1989. The effect of zinc contamination from electricity pylons: contrasting patterns of evolution in five grass species. New Phytologist 111:183–190.

AMSELLAM, L., J.L. NOYER, AND M. HOSSAERT-MCKEY. 2001. Evidence for a switch in the reproductive biology of *Rubus alceifolius* (Rosaceae) towards apomixis, between its native range and its area of introduction. American Journal of Botany 88:2243–2251.

BELNAP, L. 1995. Genetic integrity: why do we care? An overview of the issues. Pages 265–266 *in* B.A. Roundy, E.D. McArthur, J.S. Haley, and D.K. Mann, compilers, Proceedings of the wildland shrub and arid land restoration symposium. USDA, Forest Service, General Technical Report INT-315, Ogden, UT.

BLOSSEY, B., AND R. NOTZOLD. 1995. Evolution of increased competitive ability in invasive nonindigeneous species: a hypothesis. Journal of Ecology 83:887–889.

BOTTOMS, R.M., AND T.D. WHITSON. 1998. A systems approach for the management of Russian knapweed (*Centaurea repens*). Weed Technology 12:363–366.

CALLAWAY, R.M., AND E.T. ASCHEHOUG. 2000. Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. Science 290:521–523.

D'ANTONIO, C.M., AND L.A. MEYERSON. 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology 10:703–713.

DAVIS, M.A., J.P. GRIME, AND K. THOMPSON. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

DESHPANDE, A.U., G.S. APTE, R.A. BAHULIKAR, M.D. LAGU, B.G. KULKARNI, H.S. SURESH, N.P. SINGH, ET AL. 2001. Genetic diversity across natural populations of three montane plant species from the Western Ghats, India, revealed by inter-simple sequence repeats. Molecular Ecology 10:2397–2408.

DICE, L.R. 1945. Measures of the amount of ecologic association between species. Ecology 26:297–302.

DOYLE, J.J., AND J.L. DOYLE. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. Phytochemical Bulletin 19:11–15.

ELLSTRAND, N.C., AND K.A. SCHIERENBECK. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants. Proceedings of the National Academy of Science 97:7043–7050.

ELTON, C.S. 1958. The ecology of invasions by animals and plants. Methuen, London.

FRYXELL, P.A. 1957. Mode of reproduction of higher plants. Botanical Review 23:135–233.

GITZENDANNER, M.A., AND P.S. SOLTIS. 2000. Patterns of genetic variation in rare and widespread plant congeners. American Journal of Botany 87:783–792.

GOODWIN, J.R., P.S. DOESCHER, L.E. EDDLEMAN, AND D.R. ZOBEL. 1999. Persistence of Idaho fescue on degraded sagebrush-steppe. Journal of Range Management 52:187–198.

GORDON, D.R. 1998. Effects of invasive, non-indigeneous plant species on ecosystem processes: lessons from Florida. Ecological Applications 8:975–989.

GUPTA, M., Y.-S. CHYI, J. ROMERO-SEVERSON, AND J.L. OWEN. 1994. Amplification of DNA markers from evolutionarily diverse genomes using single primers of simple-sequence repeats. Theoretical and Applied Genetics 89:998–1006.

HARPER, H.L. 1977. Population biology of plants. Academic Press, New York.

HILD, A.L., B. CHRISTENSEN, AND A. MAIER. 1999. Wyoming big sagebrush seedling growth and maternal plant stand position. *In:* E.D. McArthur, W.K. Ostler, and C.L. Wambolt, compilers, Proceedings: shrubland

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

HOELZEL, A.R., AND G.A. DOVER. 1991. Molecular genetic ecology. Oxford University Press, Oxford, United Kingdom.

JONES, T.A., AND D.A. JOHNSON. 1998. Integrating genetic concepts into planning rangeland seedings. Journal of Range Management 51:594–606.

JONES, T.A., AND D.C. NIELSON. 1989. Self-compatibility in 'Paloma' Indian ricegrass. Journal of Range Management 42:187–190.

LARSON, S.R., B.L. WALDRON, S.B. MONSEN, L. ST. JOHN, A.J. PALAZZO, C.L. MCCRACKEN, AND R.D. HARRISON. 2001. AFLP variation in agamospermous and dioecious bluegrasses of Western North America. Crop Science 41:1300–1305.

LEVINE, J.M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854.

LEVINE, J.M., AND C.M. D'ANTONIO. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26.

LINHART, Y.B. 1995. Restoration, vegetation, and the importance of genetic and evolutionary perspectives. Pages 271–287 *in* B.A. Roundy, E.D. McArthur, J.S. Haley, and D.K. Mann, compilers, Proceedings of the wildland shrub and arid land restoration symposium. USDA, Forest Service, General Technical Report INT-315, Ogden, UT.

LINHART, Y.B., AND M.C. GRANT. 1996. Evolutionary significance of local genetic differentiation in plants. Annual Review of Ecology and Systematics 27: 237–277.

MADRITCH, M.D., AND M.D. HUNTER. 2002. Phenotypic diversity influences ecosystem functioning in an oak sandhills community. Ecology 83:2084–2090.

MCGUINNIES, W.J., W.A. LAYCOCK, T. TSUCHIYA, C.M. YONKER, AND D.A. EDMUNDS. 1998. Variability within a native stand of blue grama. Journal of Range Management 41:391–395.

MEEKINS, J.F., H.E. BALLARD, JR., AND B.C. MCCARTHY. 2001. Genetic variation and molecular biogeography of a North American invasive plant species (*Alliaria petiolata*, Brassicaceae). International Journal of Plant Science 162:161–169.

MOONEY, H.A., AND E.E. CLELAND. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Science 98:5446–5451.

NOAA. 2003. http://www.ncdc.noaa.gov/oa/climate/stationlocator.html.

NEI, M. 1987. Molecular evolutionary genetics. Columbia University Press, New York.

PARTEL, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. Ecology 83: 2361–2366.

ROHLF, F.J. 1989. NTSYS-pc numerical taxonomy and multivariate analysis system. Exeter Publishing, Setauket, New York.

ROUNDY, B.A., N.L. SHAW, AND D.T. BOOTH. 1997. Using native seeds on rangelands. Pages 1–8 *in* N.L. Shaw and B.A. Roundy, compilers, Proceedings: using seeds of native species on rangelands. USDA, Forest Service, General Technical Report INT-GTR-372, Rapid City, SD.

SAS INSTITUTE. 1999. SAS/STAT user's guide, release 8.0. Cary, NC.

SHANNON, C.E., AND W. WEAVER, 1949. The mathematical theory of communication. University of Illinois, Urbana.

SHELEY, R., AND J. STIVERS. 1999. Whitetop. *In:* R.L. Sheley and J.K. Petroff, editors, Biology and management of noxious rangeland weeds. Oregon State University Press, Corvallis.

SIEMANN, E., AND W.E. ROGERS. 2001. Genetic differences in growth of an invasive tree species. Ecology Letters 4:514–518.

SNAYDON, R.W., AND T.M. DAVIES. 1982. Rapid divergence of plant populations in response to recent changes in soil conditions. Evolution 36:289–297.

STENSTROM, A., B.O. JONSSON, I.S. JONSDOTTIR, T. FAGERSTROMS, AND M. AUGNER. 2001. Genetic variation and clonal diversity in four clonal sedges (*Carex*) along the Arctic coast of Eurasia. Molecular Ecology 10:497–513.

THOMPSON, J.D. 1999. Population differentiation in Mediterranean plants: insights into colonization history and the evolution and conservation of endemic species. Heredity 82:229–236.

TUTHILL, D.E., AND G.K. BROWN. 2003. Inter-simple sequence repeat (ISSR) variation in three populations of *Gaura neomexicana* spp. *coloradoensis* (Onagraceae), F.E. Warren Air Force Base, Cheyenne, Wyoming. Western North American Naturalist 63: 251–257.

WATSON, A.K. 1980. The biology of Canadian weeds. 43. *Acroptilon* (*Centaurea*) *repens* (L.) DC. Canadian Journal of Plant Science 60:993–1004.

WHITLOCK, M.C. 1997. Founder effects and peak shifts without genetic drift: adaptive peak shifts occur easily when environments fluctuate slightly. Evolution 51:1044–1048.

WHITSON, T.D. 1999. Russian knapweed. *In:* R.L. Sheley and J.K. Petroff, editors, Biology and management of noxious rangeland weeds. Oregon State University Press, Corvallis.

WOLFE, A.D., AND A. LISTON. 1998. Contributions of PCR-based methods to plant systematics and evolutionary biology. Pages 43–86 *in* D.E. Soltis, P.S. Soltis, and J.J. Doyle, editors, Molecular systematics of plants, II. Kluwer, Boston, MA.

WOLFE, A.D., Q.-Y. XIANG, AND S.R. KEPHART. 1998. Diploid hybrid speciation in *Penstemon* (Scrophulariaceae). Proceedings of the National Academy of Science. 95:5112–5115.

YEH, F.C., R.C. YANG, T. BOYLE, Z.H. YE, AND J.X. MAO. 1997. POPGENE, the user-friendly shareware for population genetic analysis. Molecular Biology and Biotechnology Centre, University of Alberta, Canada.

ZHOU, Z.H., M. MIWA, AND T. HOGETSU. 1999. Analysis of genetic structure of a *Suillus grevillei* population in a *Larix kiaemferi* stand by polymorphism of inter-simple sequence repeat (ISSR). New Phytologist 144: 55–63.

ZIETKIEWICZ, E., A. RAFALSKI, AND D. LABUDA. 1994. Genome fingerprinting by simple sequence repeat (SSR)–anchored polymerase chain reaction amplification. Genomics 20:176–183.

Received 16 July 2003
Accepted 13 April 2004