Roads as Conduits for Exotic Plant Invasions in a Semiarid Landscape

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Abstract: *Roads are believed to be a major contributing factor to the ongoing spread of exotic plants. We examined the effect of road improvement and environmental variables on exotic and native plant diversity in roadside verges and adjacent semiarid grassland, shrubland, and woodland communities of southern Utah (U.S.A.). We measured the cover of exotic and native species in roadside verges and both the richness and cover of exotic and native species in adjacent interior communities (50 m beyond the edge of the road cut) along 42 roads stratified by level of road improvement (paved, improved surface, graded, and four-wheel-drive track). In roadside verges along paved roads, the cover of* Bromus tectorum *was three times as great (27%) as in verges along four-wheel-drive tracks (9%). The cover of five common exotic forb species tended to be lower in verges along four-wheel-drive tracks than in verges along more improved roads. The richness and cover of exotic species were both more than 50% greater, and the richness of native species was 30% lower, at interior sites adjacent to paved roads than at those adjacent to four-wheel-drive tracks. In addition, environmental variables relating to dominant vegetation, disturbance, and topography were significantly correlated with exotic and native species richness and cover. Improved roads can act as conduits for the invasion of adjacent ecosystems by converting natural habitats to those highly vulnerable to invasion. However, variation in dominant vegetation, soil moisture, nutrient levels, soil depth, disturbance, and topography may render interior communities differentially susceptible to invasions originating from roadside verges. Plant communities that are both physically invasible (e.g., characterized by deep or fertile soils) and disturbed appear most vulnerable. Decision-makers considering whether to build, improve, and maintain roads should take into account the potential spread of exotic plants.*

Caminos como Conductos para Invasiones de Plantas en un Paisaje Semiárido

Resumen: *Se piensa que los caminos son un factor importante que contribuye a la continua dispersión de plantas exóticas. Examinamos el efecto del mejoramiento de caminos y variables ambientales sobre la diversidad de plantas exóticas y nativas en bordes de caminos y comunidades adyacentes de pastizales semiáridos, matorrales y bosques en el sur de Utah (E.U.A). Medimos la cobertura de especies exóticas y nativas en los bordes de caminos así como la riqueza y cobertura de especies exóticas y nativas en comunidades interiores adyacentes (50 m del borde del camino) a lo largo de 42 caminos estratificados por el nivel de mejoramiento (pavimentada, superficie mejorada, escalonada y camino para vehículos de doble tracción). En los bordes de caminos pavimentados, la cobertura de* Bromus tectorum *fue tres veces mayor (27%) que en bordes a los largo de caminos para vehículos de doble tracción (9%). La cobertura de cinco especies comunes de hierbas exóticas tendió a ser menor en bordes a lo largo de caminos para vehículos de doble tracción que en bordes a lo largo de caminos mejorados. La riqueza y cobertura de especies exóticas fueron más de 50% mayor, y la riqueza de especies nativas fue 30% menor, en sitios interiores adyacentes a caminos pavimentados que en los adyacentes a caminos para doble tracción. Adicionalmente, las variables ambientales relativas a la vegetación dominante, perturbación y topografía estuvieron significativamente correlacionadas con la riqueza y cobertura de especies exóticas y nativas. Los caminos mejorados pueden actuar como conductos*

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para la invasión de ecosistemas adyacentes al convertir hábitats naturales en sitios altamente vulnerables a la invasión. Sin embargo, la variación en la vegetación dominante, humedad del suelo, niveles de nutrientes, profundidad de suelo, perturbación y topografía pueden hacer que las comunidades interiores sean diferencialmente susceptibles a invasiones originadas en los bordes de caminos. Las comunidades de plantas que físicamente propensas a la invasión (por ejemplo, caracterizadas por suelos profundos o fértiles) así como perturbables, parecen ser más vulnerables. Los tomadores de decisiones que consideren construir, mejorar y mantener caminos deben tener en cuenta los efectos potenciales de la expansión de plantas exóticas.

Introduction

Roads provide a major conduit for the spread of exotic plants into natural areas, particularly in arid and semiarid landscapes of the American West, where exotic annual grasses and forbs pose a major conservation challenge (U.S. Bureau of Land Management [BLM] 1999). Exotic grasses such as cheatgrass (*Bromus tectorum*) and forbs such as knapweeds (Centaurea species) have invaded over 50 million ha of the region, reducing biodiversity by displacing native plants and animals (Mack 1989; Billings 1990; BLM 1999). Although roads have been implicated as an important factor contributing to the spread of exotic plants (Tyser & Worley 1992; Forman 2000; Parendes & Jones 2000; Trombulak & Frissell 2000), this effect remains poorly studied.

Declines in the presence of exotic species with distance from roads have been observed in Glacier National Park (U.S.A.) (Tyser & Worley 1992), California (Frenkel 1970; Gelbard & Harrison in press), and the Mojave Desert (Johnson et al. 1975). A number of mechanisms have been proposed as explanations for these patterns. Vehicles and road-fill operations transport exotic plant seeds into uninfested areas, and road construction and maintenance operations provide safe sites for seed germination and seedling establishment (Schmidt 1989; Lonsdale & Lane 1994; Greenberg et al. 1997; Trombulak & Frissell 2000). Clearing of vegetation and soils during construction, addition of roadfill, and grading of unpaved roads create areas of bare and deeper soil that allow exotic seeds to become established (Frenkel 1970; Trombulak & Frissell 2000). Mowing roadside verges may favor exotic plant species that are less sensitive to clipping than native flora (Forman & Alexander 1998; Benefield et al. 1999). Similarly, roadside herbicide treatments that reduce the cover of some exotic species may favor others and at the same time reduce the cover of native species (Tyser et al. 1998). Compaction by vehicles contributes to roadside invasions by reducing native plant vigor and creating areas of competition-free space that are open to invasion (Frenkel 1970). Thus, plant communities adjacent to more improved roads (e.g., paved, gravel) that receive high vehicle traffic might be expected to be more invaded than those adjacent to infrequently used primitive roads (e.g., four-wheel-drive tracks) (Parendes & Jones 2000).

Semiarid grasslands, shrublands, and woodlands of the Colorado Plateau (U.S.A.) are a good setting for examining the effects of road improvement because of the rapid proliferation of both roads and exotic plants throughout these habitats (BLM 1999). In the past 100 years, the region's native flora has become increasingly threatened by invading Mediterranean annual grasses (e.g., *Bromus tectorum*) and forbs (e.g., *Centaurea*, *Halogeton*, *Erodium* species) (Mack 1989; BLM 1999). The vegetation composition of relict and long-ungrazed sites (e.g., Kindschy 1994; Anderson & Inouye 2001) suggests that livestock have played a major role in this invasion (Belsky & Gelbard 2000), but alteration of the fire regime (Billings 1990; BLM 1999), extremes in annual precipitation (Anderson & Inouye 2001), and the expansion of road networks (Forman 2000) have undoubtedly contributed to the plant invasions as well. The mechanistic basis for these invasions has been well-documented in experimental studies. Exotic annuals are not only more tolerant of livestock grazing (Mack 1989; Roché et al. 1994) and fire (Billings 1990; BLM 1999) but consistently outcompete native species for water (Harris 1967). However, a key unanswered question is whether the high concentration of exotic plants along roads is a general phenomenon or whether some roads are more likely than others to act as conduits for exotic plant invasions.

One possible factor that may influence the effect of roads on the spread of exotic plants is the level of road improvement (Tyser & Worley 1992; Parendes & Jones 2000), which spans a gradient including ungraded four-wheel-drive tracks, graded unpaved roads, graded roads that have received surface additions, and paved roads. Effects from this range of road improvements also follow a gradient of increasing traffic levels, habitat alteration during construction, and frequency of disturbance by vehicles and road maintenance. Anecdotally, it appears that zones of weedy vegetation along more-improved roads are wider than those along primitive roads. The positive correlation between land area and species richness (Connor & McCoy 1979) may mean that verges along more-improved roads could support a greater diversity of exotic species than the relatively narrow verges adjacent to primitive roads. Verges along more-improved roads may be subjected to frequent disturbance by vehicles and road maintenance. Roadfill additions or berms created by graders may create different soil depths, chemistry, and/

or textures, which may allow invasive exotic species to become established in habitats that are otherwise inhospitable as a result of shallow, coarse, or otherwise infertile soils. Paved roads are also designed to shed water into roadside verges, which may increase the vulnerability of verges to invasion by improving moisture and nutrient availability (Johnson et al. 1975; Holzaphel & Schmidt 1990).

If more-improved roadside verges are more likely to be invaded, adjacent interior communities might also be expected to contain more exotic plants. However, environmental variables related to topography (Billings 1990; Gelbard 1999), disturbance (Hobbs & Huenneke 1992; Belsky & Gelbard 2000; Stohlgren et al. 2001; Williamson & Harrison 2002), dominant vegetation or plant community type (Larson et al. 2001), and soil resource availability (Stohlgren et al. 1999, 2001; Williamson & Harrison 2002) may also influence exotic species richness and cover in adjacent natural ecosystems. Thus, although it is well known that roadside verges tend to be highly invaded habitats, a number of questions related to the effect of road improvement remain unanswered. First, do roadside verge and interior habitats adjacent to improved roads contain more exotic species and fewer native species than those adjacent to primitive roads? Second, can any apparent effects of road improvement be explained by disturbance, dominant vegetation, or other forms of environmental variation? We examined the distribution of native and exotic plants near roads in semiarid communities of southern Utah (U.S.A.) to test the hypothesis that roadside verge and interior communities adjacent to improved roads contain more exotic species and fewer native species than those adjacent to primitive roads.

Methods

Site Description

We conducted our study in representative vegetation, soil, topographic, and disturbance conditions of Canyonlands National Park, southern Utah (lat. 38°15′N, long. 109°52′W), and in surrounding public grasslands, shrublands, and woodlands. Climate in the area is semiarid to arid, with precipitation averaging 200–250 mm/year and elevation ranging from 1300 to 2500 m. Geological substrates are sedimentary sandstones and shales, and soils are mainly loamy fine sands and sandy loams. At lower elevations (<1500 m), dominant vegetation is *Coleogyne ramosissima* on shallow sandstone-derived soils; *Atriplex confertifolia*, *Atriplex canescens*, or *Sarcobatus vermiculatus* on shale-derived saline soils; and grasslands on deeper alluvial and colluvial nonsaline soils. Dominant grasses include *Stipa comata* (also *Hesperostipa comata*; Welsh et al. 1993), *Stipa hymenoides* (also *Achnatherum hymenoides*), *Hilaria jamesii*, and, in more disturbed sites, the exotic *Bromus tectorum*. At intermediate elevations (1500–2300 m), communities are dominated by *Artemisia tridentata* shrublands that may also include *Bouteloua gracilis* and *Agropyron desertorum*, an exotic bunchgrass that has been introduced as livestock forage. Woodlands containing *Juniperus osteosperma* and *Pinus edulis* occur in both vegetation zones, especially on skeletal soils (West 1983). Biological soil crusts composed of lichens, mosses, algae, and cyanobacteria cover the soil surface between individual grasses, shrubs, and trees, except on exceptionally rocky sites and in areas where they have been destroyed by disturbance (Belnap & Lange 2001). Canyonlands National Park has been protected from extractive activities since 1964. Surrounding public lands continue to be managed for multiple uses, including domestic livestock grazing, outdoor recreation, mining, and oil and gas extraction.

Site-Selection Protocol

We stratified roads in the study site (as detailed on a Trails Illustrated map of the area) into four categories: 1, paved; 2, improved surface (unpaved roads with surface roadfill additions); 3, graded (graded, high-clearance roads without surface roadfill); and 4, four-wheel-drive track (seldom-graded high-clearance roads that typically appear only as tire tracks) (National Geographic Maps 1997; Fig. 1). For each paved road, we located an improved- surface road, a graded road, and a four-wheel-drive track that contained comparable environmental conditions, such as similar topography, dominant vegetation, degree of rockiness, and disturbance. We avoided recently mowed sites, but with the exception of paved roads it was impossible to attain records of areas recently treated with herbicides. Total sample size was 12 paved roads, 7 improved-surface roads, 11 graded roads, and 12 four-wheel-drive tracks.

Field-Data Collection

Between early June and July 1998 we sampled 10 sites along a transect at each of the 42 roads. Along each road, we randomly selected five 0.8-km segments located between 0 and 16 km from an end of a road or an intersection. At the beginning and end of each 0.8-km segment, we conducted an extensive survey to estimate the cover of all individual native and exotic plant species along 50 m of the roadside verge (parallel to the road). Species definitions followed those of Welsh et al. (1993). Cover values of plant species followed those of Daubenmire (1959), but we added a class to account for numerous species that occupied areas with <1% cover.

We then measured the width of the roadside plant community as the distance between the outer edge of the road and the outer edge of the road cut or berm. Although no exact changes identified the edge of the road

Figure 1. Illustration of roadside plant communities adjoining the following surfaces: (a) paved, (b) improved surface, (c) graded, and (d) four-wheel-drive track.

cut, it was easily visible from alterations in vegetation cover and height and from seedbed quality (Fig. 1) and has been used in other studies (e.g., Frenkel 1970; Cale & Hobbs 1991; Tyser & Worley 1992).

Although sampling entire roadside verges resulted in unequal plot sizes within roadside plant communities, we only used these plots to examine relationships between road improvement and species cover, which unlike richness can be measured independently of plot size. We then recorded the cover and richness of plant species in interior communities within a parallel 10 × 50 m area, defining interior communities as at least 50 m from the edge of the road cut and beyond the influence of roadside disturbance. To provide a measure of soil-surface disturbance, we estimated the percent cover of biological soil crust. We also estimated the surface cover (percent) of rock.

We marked the location coordinates of each site with a global positioning system (GPS). We acquired geographic information system (GIS) data, including a digital elevation model (30-m cell size), from Canyonlands National Park and the BLM (Moab, Utah). We used the digital elevation model to extract elevation, aspect (degrees, relativized to north), and slope (percent) at each GPS point.

Statistical Analyses

We averaged measurements from the 10 sites along each road into single replicate measures before conducting statistical analyses, which we did with JMP 4.0 (SAS Institute 2000). We analyzed data for assumptions of the parametric tests that we conducted and transformed all percent values by arcsin square root. Six exotic plant species and three native species occurred in roadside verges at sufficient frequencies (as indicated by power analyses) for individual statistical analyses: the exotics *B. tectorum*, *E. cicutarium*, *H. glomeratus*, *Salsola iberica*, *Sisymbrium altissimum*, *Melilotus officianalis*, and the natives *Stipa comata*, *Stipa hymenoides*, and *Hilaria jamesii*). In interior communities, two exotic annual species (*Bromus* and *Salsola*) and three native perennial species (*S. comata*, *S. hymenoides*, and *H. jamesii*) occurred at sufficient frequencies for individual analyses.

To test whether there was an overall effect of road improvement on exotic and native species cover and whether relationships among dependent variables could alter our results, we performed multivariate analyses of variance (MANOVA). We used two tests, with dependent variables, which included roadside verges and interior communities and the mean cover of exotic and native species listed above. The independent variable was the level of road improvement.

There were substantial differences in the means and variances of the cover of different exotic species. Thus, we performed separate analyses of covariance (ANCOVAs) on each species to test whether any apparent effect of road improvement was due to environmental variation. We first performed forward stepwise model selection to reduce the large number of independent variables to those with significant main effects, repeating the process for each species in both roadside and adjacent interior communities, and for exotic and native species richness in interior communities. Independent variables included elevation, aspect (degrees relativized to north), slope steepness (%), cover of biological soil crust (%), cover of rock (%), and cover of dominant native plant species (%), including *A. tridentata*, *C. ramosissima*, *S. vermiculatus*, *A. canescens*, *A. confertifolia*, *S. comata*, *P. edulis*, and *J. osteosperma*. We selected these grass, shrub, and tree species because they were dominant at the study sites and because they represent many of the region's predominant plant communities as defined by West (1983) and as used in regional GIS land-cover maps. We then conducted ANCOVAs with resulting independent variables. Where we found a significant effect of road improvement, we used the Tukey's honest significant difference (HSD) multiple-range test to determine which pairs of means were significantly different. To test whether roadside verges and adjacent interior habitats differed in exotic and native species richness and cover, we used paired *t* tests.

To test for an indication of a biotic effect of native species on the richness and cover of exotic species in interior communities, we conducted linear regressions with native species richness as the independent variable and exotic species richness and the cover of Bromus and Salsola as dependent variables. To determine whether any effect of native species richness was due to environmental variation, we repeated the above ANCOVAs on exotic species richness and cover but included native species richness as an additional covariate.

The width of roadside verges differed among levels of road improvement. To determine whether roadside verge width is a function of road improvement or environmental factors, we used ANCOVA, following the same steps as described for previous ANCOVAs. Finally, to determine whether roadside verge width corresponded with the exotic and native species composition of interior communities, we performed multiple regressions. We followed the same steps described for ANCOVAs, with the exception that we substituted roadside verge width (m) for the level of road improvement as an independent variable. Where we found a significant effect of roadside verge width on native or exotic richness or cover, we used Pearson's correlation analyses to further quantify this relationship.

Results

Effect of Road Improvement

Road improvement significantly affected exotic species cover in both roadside verges and adjacent interior communities and significantly affected native and exotic species richness in interior communities (Table 1, Figs. 2–4). There was a significant whole-model effect of road improvement on the cover of exotic and native species within roadside verges (Wilks' $\lambda = 0.17$, df = 27, 88, $f = 2.69$, $p = 0.0003$). There was no significant whole-model effect of road improvement on exotic plant cover in interior communities (Wilks' $\lambda = 0.65$, df = 15, 95, $f = 1.07$, $p = 0.40$).

In separate analyses of the cover of individual exotic species in roadside verges, there was a significant effect of road improvement on the cover of all nine exotic and native species examined. The mean cover of *Bromus* was three times greater in verges adjacent to paved roads than in verges adjacent to four-wheel-drive tracks (Table 1; Fig. 3). The mean cover of *Sisymbrium*, *Erodium*, and *Melilotus* was greatest in verges adjacent to paved roads, but the cover of Halogeton was greatest in verges adjacent to improved surface roads, and the cover of *Salsola* was greatest in verges adjacent to improved surface and graded roads (Table 1; Fig. 3). The cover of native *Hilaria* was marginally greatest in paved roadsides, but the cover of *S. comata* and *S. hymenoides* did not differ among road types (Table 2; Fig. 4).

The cover of *Bromus* was more than three times greater in interior communities adjacent to improved surface roads than in interior communities adjacent to four-wheel-drive tracks (Table 1; Fig. 3). The cover of *Salsola* was greatest in interior communities next to improved surface roads and least in communities next to four-wheel-drive tracks (Table 1; Fig. 3). The exotic species richness of interior communities next to paved roads was more than 50% greater than that of interior commu-

Table 1. Effects of road improvement and environmental variables on exotic species richness and percent cover of selected exotic species in roadside verge and adjacent interior plant communities.[a]

Variable	*Exotic richness, interior* ($r^2 = 0.66$)	Bromus tectorum *roadside* ($r^2 = 0.34$)	Bromus tectorum *interior* ($r^2 = 0.51$)	Salsola iberica *roadside* ($r^2 = 0.23$)	Salsola iberica *interior* ($r^2 = 0.44$)	Sisymbrium altissimum, *roadside* ($r^2 = 0.47$)	Erodium cicutarium, *roadside* ($r^2 = 0.23$)	Halogeton glomeratus, *roadside* ($r^2 = 0.61$)	Melilotus officianalis, *roadside* ($r^2 = 0.42$)
Road improvement	0.04 (+)	0.005 (+)	0.0009 (+)	0.04 (+)	0.06 (+)	0.04 (+)	0.04 (+)	0.02 (+)	0.02 (+)
Elevation (m)	—	—	0.03 (+)	—	—	—	—	—	0.04 (+)
Aspect (degrees)	0.04 (−)	—	—	—	—	—	—	0.001 (+)	—
Slope (%)	—	—	—	—	0.05 (−)	—	—	—	—
Biological soil crust[b]	0.004 (−)	—	0.02 (−)	—	0.03 (−)	—	—	0.01 (−)	0.10 (−)
Rock[b]	—	—	—	—	—	—	—	—	—
Stipa comata[b]	—	—	—	—	—	—	—	—	—
Sarcobatus vermiculatus[b]	0.02 (+)	—	—	—	0.002 (+)	—	—	0.01 (+)	—
Artemisia tridentata[b]	—	—	—	—	—	—	—	—	—
Atriplex canescens[b]	—	—	—	—	—	—	—	—	—
Coleogyne ramosissima[b]	0.003 (−)	—	0.02 (−)	—	—	—	—	—	—
Pinus edulis[b]	0.0001 (−)	—	0.0001(−)	—	0.004 (−)	0.06 (−)	—	—	0.005 (+)
Juniperus osteosperma[b]	—	—	—	—	0.01 (+)	—	—	—	—

[a] *Numbers reported are* p *values from analyses of covariance and illustrate variables that remained significant after compensating for the listed covariates. Sign illustrates the direction of significant relationships between response and independent variables. Only statistically significant values are reported.*

[b] *Biological soil crust, rock, and species reflect cover values (%).*

nities adjacent to four-wheel-drive tracks (Table 1; Fig. 2). There was no effect of road improvement on the cover of *S. comata*, *S. hymenoides*, or *H. jamesii* (Table 2; Fig. 4). Native species richness was significantly greater in interior communities next to graded roads and four-wheel-drive tracks than next to paved and improved surface roads (Table 2; Fig. 2).

The width of roadside verges was greatest adjacent to paved roads and least adjacent to four-wheel-drive tracks (Fig. 5). This effect remained significant ($p < 0.0001$) after environmental variation was accounted for. Exotic species richness ($r = 0.34, p = 0.02$) and the cover of Bromus ($r = 0.48, p = 0.001$) and Salsola ($r = 0.41, p = 0.007$) in interior communities were significantly positively correlated with the width of adjacent roadside verges. Native species richness in interior communities was significantly negatively correlated ($r = -0.50, p = 0.0007$) with the width of adjacent roadside verges; these relationships remained significant after environmental variation was accounted for. The cover of *S. comata*, *S. hymenoides*, and *H. jamesii* in interiors was not correlated with the width of roadside verges.

Environmental Correlates of Exotic Species Richness and Cover

ROADSIDE VERGES

In roadside verges, exotic and native species cover tended to be correlated with few environmental variables (Tables 1 & 2). *Sisymbrium* cover was marginally negatively correlated with the cover of *Pinus* in the adjacent interior community. The cover of *Halogeton* was positively correlated with aspect (relative to north) and the cover of *Sarcobatus* and negatively correlated with biological soil crust cover in the adjacent interior community. The cover of *Melilotus* was positively correlated with elevation and *Pinus* cover and marginally negatively correlated with the cover of biological soil crust in the interior community. The percent cover of *Erodium* and *Salsola* in roadside verges was not correlated with any environmental variables. The cover of exotic species tended to be greater in roadside verges than in adjacent interior communities (Figs. 3 & 4).

The cover of *S. comata* in roadsides was strongly positively correlated with its cover in interiors (Table 2). The cover of *S. hymenoides* was positively correlated with the cover of *S. comata* and Juniperus in interiors. The cover of *Hilaria* was positively correlated with elevation, negatively correlated with the cover of *Pinus*, and marginally negatively correlated with the cover of Atriplex. The cover of native species tended to be greater in interior communities than in roadside verges (Figs. 3 & 4).

INTERIOR COMMUNITIES

The cover of the exotics *Bromus* and *Salsola* and the natives *S. comata* and *S. hymenoides* were significantly

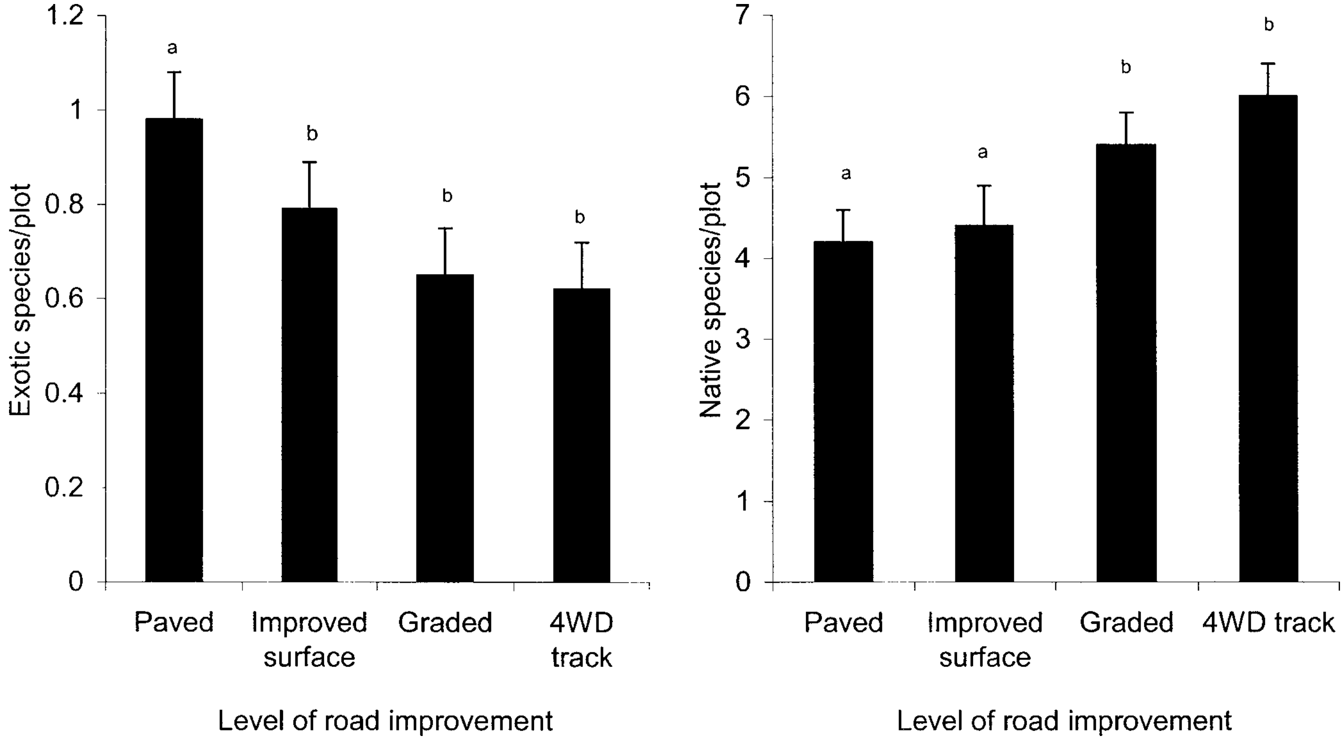

Figure 2. Exotic and native species richness in interior communities along paved, improved-surface, graded, and four-wheel-drive (4WD) roads. Error bars represent 1 SE. Different letters indicate significant differences ($p < 0.05$*) among levels of road improvement in Tukey's honest significant difference multiple-range tests; overall significance of effects indicated by analysis of covariance (Tables 1 & 2).*

correlated with more environmental variables in interior communities than in roadside verges (Tables 1 & 2). Exotic species richness was negatively correlated with aspect and the cover of biological soil crust, Pinus, and Coleogyne and positively correlated with the cover of Sarcobatus (Table 1). The cover of *Bromus* was negatively correlated with the cover of biological soil crust, *Pinus*, and *Coleogyne* and positively correlated with elevation. The cover of *Salsola* was negatively correlated with slope steepness and the cover of biological soil crust, *Pinus*, and *Atriplex*, whereas it was positively correlated with the cover of *Sarcobatus* and *Juniperus*. Exotic species richness and the cover of *Bromus* were inversely correlated ($p < 0.05$) with native species richness. When we compensated for environmental variation, however, there was no effect of native species richness on exotic species richness or cover.

Native species richness was positively correlated with the cover of biological soil crust and *S. comata* and marginally positively correlated with slope steepness (Table 2). The cover of *S. comata* was significantly positively correlated with the cover of biological soil crust and inversely correlated with the cover of Sarcobatus and Pinus. The cover of *S. hymenoides* was negatively correlated with the cover of Sarcobatus, and the cover of *Hilaria* was significantly negatively correlated with the cover of Juniperus.

Discussion

Roadside verges adjacent to paved and improved surface roads contained a greater cover of both exotic and native species than verges adjacent to four-wheel-drive tracks. Interior communities adjacent to paved and improved surface roads contained a greater richness and cover of exotic species and lower richness and cover of native species than interior sites adjacent to four-wheel-drive tracks. Our results therefore indicate that the effect of road improvement differs between roadside verges and adjacent interior communities. In roadside verges, the improvement gradient from four-wheel-drive tracks to paved roads corresponded with increasing cover of both exotic and native species. But in interior communities, improvement of adjacent roads corresponded with greater cover and richness of exotic species and lower richness of native species. These results persisted when we included in our models a large number of environmental covariates, representing such potentially confounding factors as topography, disturbance, rockiness, and cover of dominant native grass, shrub, and tree species. Our findings are consistent with the idea that the effect of road improvement on plant cover and richness is due to factors associated with road construction, road maintenance, and vehicle traffic, not to differences in site characteris-

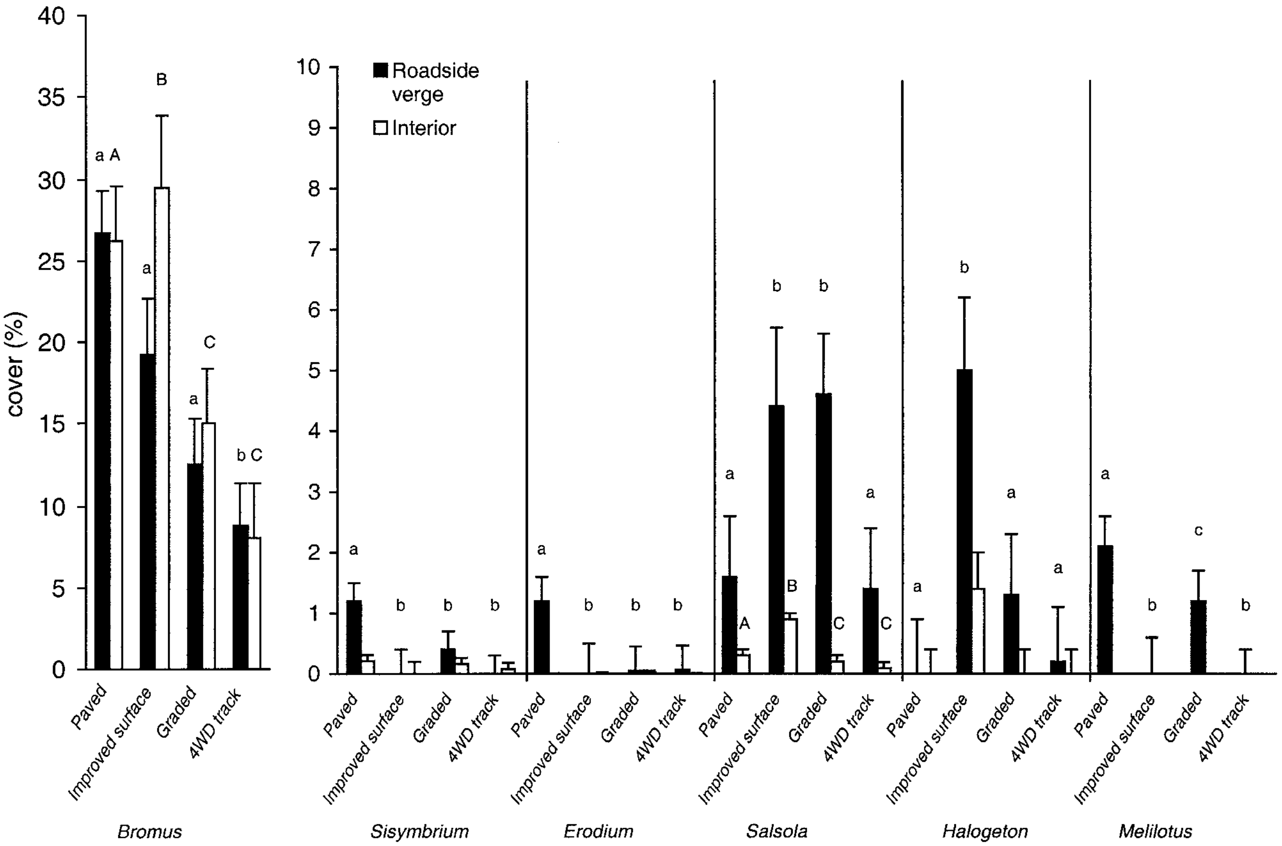

Figure 3. Percent cover of Bromus tectorum *and selected exotic forb species in roadside and interior communities along paved, improved-surface, graded, and four-wheel-drive (4WD) roads. Error bars represent 1 SE. Different letters (ab for roadside verges, ABC for interior communities) indicate significant differences (*p *< 0.05) among levels of road improvement in Tukey's HSD multiple-range tests; overall significance of effects indicated by analysis of covariance (Table 1).*

tics. It thus appears that improvement of four-wheel-drive tracks increases the richness and cover of exotic species and reduces the richness of native species in adjacent interior ecosystems.

Of the nine species we examined, seven were most abundant in verges adjacent to paved roads. In contrast, all exotic species were least abundant or showed <1% cover in verges adjacent to four-wheel-drive tracks. Of these exotics, *Bromus* and *Halogeton* pose a major threat to native species and ecosystem processes (Billings 1990; BLM 1999). Native species also showed their greatest cover in the most improved roadsides, suggesting that in these semiarid roadside verges, native cover is too sparse to limit the establishment of introduced exotic species.

Although we did not measure exotic species richness and cover in sites with no roads as a control, we observed anecdotally that sites isolated (>1000 m) from roads tended to contain fewer exotic species than sites near (<50 m from) roads, a situation that Gelbard and Harrison (in press) have since documented in California grasslands. Both the construction of new roads and the improvement of existing roads appear to be important factors in the ongoing spread of exotic plants throughout this landscape.

We found a significant effect of road improvement on both exotic and native species richness in interior communities 50 m beyond the edge of the road cut, suggesting that road improvement influences the distribution of both exotic and native species in lands beyond the influence of roadside disturbance. Exotic species richness tended to be greater and native species richness tended to be lower next to more improved roads, although we caution that our measurements of richness were a snapshot. We surveyed each site only once during a year of below-normal spring precipitation and therefore probably underestimated richness, especially of native annuals.

In addition to the effects of road improvement, numerous environmental covariates showed significant correlations with the cover of exotic and native species in roadside verges and, especially, with the cover and richness of exotic and native species in interior communities. For

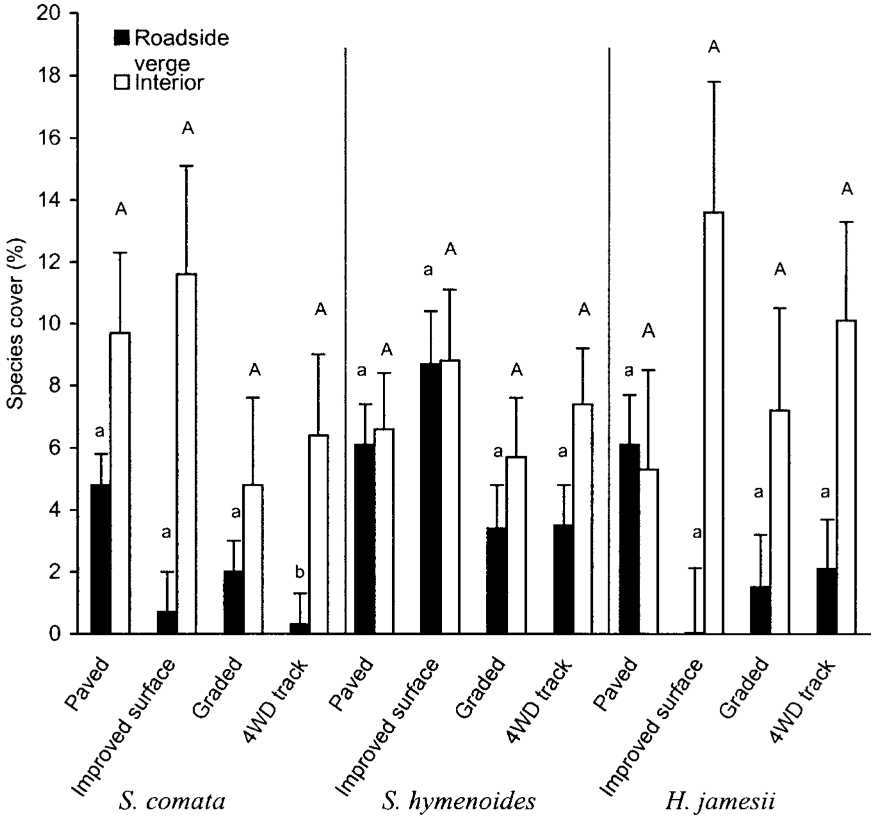

*Figure 4. Percent cover of selected native grass species in roadside and interior communities along paved, improved-surface, graded, and four-wheel-drive (4WD) roads. Error bars represent 1 SE. Different letters (ab for roadside verges, AB for interior communities) indicate significant differences (*p *< 0.05) among levels of road improvement in Tukey's HSD multiple-range tests; overall significance of effects indicated by analysis of covariance (Table 2).*

the most part, these patterns are consistent with the findings of previous studies (e.g., Stohlgren et al. 2001). For example, in interior communities there was a general tendency for exotic species to be less prevalent on sites containing greater biological soil-crust cover. They were also less prevalent at sites with higher cover of *Coleogyne* and *Pinus*, whose presence serves as an indicator of shallow or coarse soils (West 1983). Communities containing high cover of Sarcobatus, an indicator of saline soils with a shallow water table (West 1983), also tended to contain high richness and cover of exotic species, especially of Salsola and the halophyte *Halogeton*. These findings indicate that the ability of an invasive species to spread from a roadside depends on the soil

Table 2. Effects of road improvement and environmental variables on native species richness and percent cover of selected native species in roadside verge and adjacent interior plant communities.[a]

	Native richness	Stipa comata		Stipa hymenoides		Hilaria jamesii	
Variable	*interior* (r^2 = *0.51)*	*roadside* (r^2 = *0.55)*	*interior* (r^2 = *0.45)*	*roadside* (r^2 = *0.46)*	*interior* (r^2 = *0.21)*	*roadside* (r^2 = *0.37)*	*interior* (r^2 = *0.20)*
Road improvement	0.006 (−)	0.002 (+)	—	—	—	0.09 (+)	—
Elevation (m)	—	—	—	—	—	0.02 (+)	—
Aspect (degrees)	—	—	—	—	—	—	—
Slope (%)	0.09 (+)	—	—	—	—	—	—
Biological soil crust[b]	0.04 (+)	—	0.008 (+)	—	—	—	—
Rock[b]	—	—	—	—	—	—	—
Stipa comata[b]	0.01(+)	0.0001 (+)	—	0.06 (+)	—	—	—
Artemisia tridentata[b]	—	—	—	—	—	—	—
Sarcobatus vermiculatus[b]	—	—	0.004 (−)	—	0.07 (−)	—	—
Atriplex canescens[b]	—	—	—	—	—	0.08 (−)	—
Coleogyne ramosissima[b]	—	—	—	—	—	—	—
Pinus edulis[b]	—	—	0.04 (−)	—	—	0.01 (−)	—
Juniperus utahensis[b]	—	—	—	0.03 (+)	—	—	0.03 (−)

[a] *Numbers reported are* p *values from analyses of covariance and illustrate variables that remained significant after compensating for the listed covariates. Sign illustrates the direction of significant relationships between response and independent variables. Only statistically significant values are reported.*

[b] *Biological soil crust, rock, and species reflect cover values (%).*

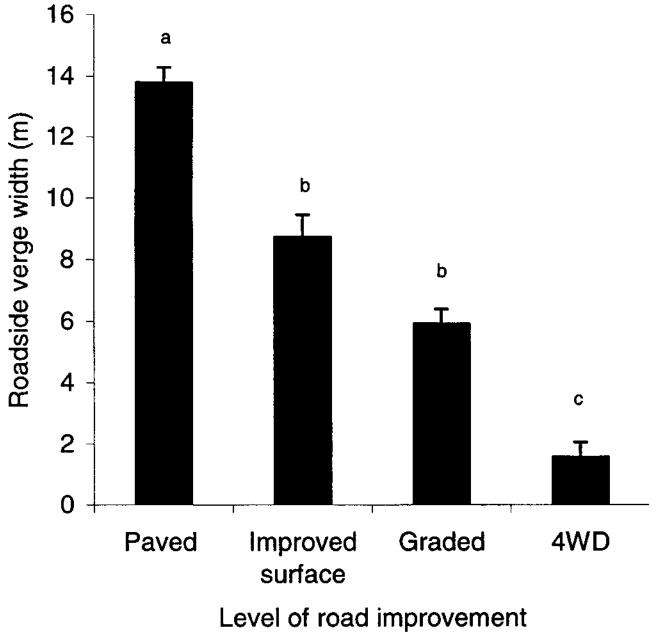

Figure 5. Width of roadside verges (for both sides of the road) among levels of road improvement (4WD, four-wheel-drive). Error bars represent 1 SE. Different letters indicate significant differences ($p < 0.05$*) among levels of road improvement in Tukey's HSD multiple-range test; overall significance of effect indicated by analysis of covariance.*

characteristics of the adjacent community: if they are favorable for invaders present in the roadside and soils are disturbed, an invasion will generally occur (Williamson & Harrison 2002).

Overall, the factor that most consistently and significantly exerted an effect on the cover of exotic species within roadside verges was the level of road improvement. It is not surprising that this factor exerted the greatest relative influence on roadside plant community composition because the level of road improvement serves as an indicator of the frequency of exotic plant seed introductions by vehicles and roadfill, the frequency of disturbances to native vegetation and soils by vehicles and road maintenance, the soil depth of the roadside, altered soil chemistry or texture of roadside fill, and the amount of water movement into the roadside. In addition, our results suggest a possible area effect: the larger size of roadside verges along more improved roads may support greater cover of both exotic and native species.

On the other hand, the factors that exerted the most consistent and significant negative effect on the richness and cover of exotic species in interior communities were biological soil-crust cover and, especially, the cover of dominant plants that are indicators of shallow, rocky, and infertile soils (West 1983). The cover of both *Pinus* and *Coleogyne* was strongly negatively correlated with exotic species richness and cover, suggesting that interior communities near roads are less vulnerable to invasion where soils are characterized by low moisture availability, shallow depth, and/or low nutrient levels (Safford & Harrison 2001; Williamson & Harrison 2002). The cover of Pinus was also inversely correlated with the cover of the native grass *S. comata*, which supports the idea that communities containing a low abundance of native species may be resistant to invasion (Stohlgren et al. 2001).

We found a significant negative relationship between the richness of native species and the richness and cover of exotic species in interior communities, but this effect was not significant when environmental variation was accounted for. In contrast to other studies (e.g., Tilman 1997; Anderson & Inouye 2001), our results do not provide evidence for an effect of native species on the richness or cover of exotic species. Rather, they support the idea that, at larger spatial scales, relationships between native and exotic species richness may correspond with environmental variation (Levine 2000). In these semiarid communities, native perennial plants are widely spaced and have roots deep in the soil profile (Belnap & Phillips 2001) and thus may leave sufficient surface moisture available to be used by an exotic annual if it can become established. In a sagebrush steppe landscape, however, Anderson and Inouye (2001) found no relationship between native and exotic species richness but instead found a negative relationship between the total cover of native species and the richness of exotic species. The scale of our study may have been too coarse to detect a biotic effect of native species on exotic species (Levine 2000).

Biological soil-crust cover was negatively correlated with exotic species richness and the cover of *Bromus* and *Salsola* but positively correlated with native species richness and the cover of *S. comata*. This relationship may indicate a direct facilitation of native species and exclusion of non-native species by biological soil crusts. In addition, because biological soil crusts are readily destroyed by trampling or vehicles, they can be used as a surrogate measure for soil surface disturbance. As such, they suggest a positive relationship between soil surface disturbance and exotic species richness and cover and a negative relationship between disturbance and native species richness and cover. These findings agree with those of Stohlgren et al. (2001), who observed a strong inverse correlation between exotic species richness and cover of biological soil crust. One implication of this finding is that plant communities near roads experiencing more disturbance and/or having less biological soil crust cover are more vulnerable to invasion. Another implication is that biological soil crusts may act as a physical or chemical barrier to the establishment and growth of some exotic species and in turn may help protect native species (Mack 1989; Kaltenecker et al. 1999; Belnap et al. 2001; Stohlgren et al. 2001). As with the effect of road improvement, our findings suggest that these effects may be most pronounced in communities that are sufficiently invasible to allow exotic invaders to become established, spread, and suppress native reproduction (Harris 1967; Billings 1990) or alter ecosystem processes (Billings 1990; BLM 1999). Experiments are clearly needed to determine the causes and implications of these patterns.

Exotic plants do not always spread from invaded roadside corridors, even when their seeds are readily available from the roadside and when adjacent interior communities are disturbed. Physical site factors related to soils and topography must first be favorable before an exotic plant invasion can occur. In semiarid landscapes, resource-poor soils appear to be most resistant to invasion (Belnap & Phillips 2001; Safford & Harrison 2001; Stohlgren et al 1999, 2001; Williamson & Harrison 2002). This contrasts with the findings of studies in more mesic ecosystems (Tilman 1997).

Also intriguing was the effect of roadside verge width, which was largely a function of road improvement. The width of roadside verges was strongly positively correlated with exotic species richness and the cover of Bromus and Salsola in interior communities and strongly negatively correlated with native species richness in interior communities. This highly significant relationship between road improvement, roadside verge width, and exotic plant invasion in interior communities may be explained in part by an area effect (Connor & McCoy 1979): wider roadsides create more disturbed habitat in which native vegetation has been removed. In turn, these larger roadsides may support more individuals of an exotic species, and these larger populations of roadside weeds may be more likely to survive, reproduce, and spread into interior communities as a result of greater pollen availability, seed production, and genetic diversity (Barret 2000).

It is likely, however, that factors that we did not measure contributed to the relationship between road improvement, roadside verge width, and exotic plant invasions. First, more-improved roads with wider roadside verges may be more likely to act as moisture reservoirs than unsealed primitive roads by reducing evaporation from beneath roads and by concentrating infiltration into roadside verges (Johnson et al. 1975; Holzaphel & Schmidt 1990). More-improved roads also receive more seed introductions, seedbed alterations, and disturbance by vehicle traffic and road-maintenance operations, and their verges may contain deeper, finer textured, or more fertile soils as a result of roadfill additions (Greenberg et al. 1997). In addition, road designs and maintenance operations may increase both exotic and native species richness and cover by creating multiple habitat zones within verges, and different zones may support different species (Frenkel 1970; Bugg et al. 1997). In some cases, more-improved roads may be older than primitive roads, and the vegetation adjacent to them may therefore have been subjected to disturbance and the introduction of exotic plant seeds for a longer period of time. Unfortunately, data on traffic levels, road-maintenance schedules, road design and age, and time since last improvement were available only for paved roads and thus could not be considered.

Conclusions and Management Implications

We have demonstrated that as roads are improved from four-wheel-drive tracks to paved roads, the verges adjacent to them tend to become wider and to contain an increasing cover of exotic plant species. Each step of road improvement would appear to convert an increasing area of natural habitat to roadside habitat, a finding with considerable implications when extrapolated to the landscape scale. For example, our results suggest that improving 10 km of four-wheel-drive tracks to paved roads converts an average of 12.4 ha of interior habitat to roadside plant communities that typically contain a substantially greater richness and cover of exotic species than the habitat that they replace as land cover. The 117,205 km of rural paved roads in the state of Utah alone (U.S. Department of Transportation 1999) may have already converted as much as 164,087 ha of land from interior to roadside plant communities. Thus, road improvement can be considered a major agent of land-cover change, converting natural habitat to roadside habitat that tends to be highly invaded and may act as a conduit for the invasion of adjacent interior ecosystems (Tyser & Worley 1992; Forman 2000).

Because Gelbard (1999) observed similar patterns in Grand Staircase Escalante National Monument in south-central Utah and Great Basin National Park in eastern Nevada, we speculate that these effects may apply to other semiarid landscapes. Clearly, roads should be considered important targets of both local and regional efforts to prevent and control exotic plant invasions. The process of deciding whether and how to improve, build, or maintain a road must include consideration of effects on the spread of exotic plants.

One positive finding of our study is that the prevention of invasion in this semiarid landscape, still the best tool for effective weed management (e.g., Hobbs & Humphries 1995; Mack et al. 2000), remains a viable option in many areas. For example, aside from Bromus and exotic grasses intentionally introduced in the past, we recorded the majority of exotic plants within roadside verges and other disturbed lands such as chainings and areas near livestock water sources and salt licks. In the case of some species such as Salsola and Sisymbrium, this suggests a low potential for spread away from roads. For species demonstrated to have greater potential to spread, such as *Bromus* and knapweeds (Billings 1990; Tyser & Worley 1992), our findings suggest that major opportunities remain to prevent exotic plant invasions in this semiarid landscape by minimizing the construction of new roads and the improvement of existing roads.

Where such activities are necessary, the spread of exotic plants can be reduced if road designers take appropriate measures such as minimizing the soil depth of roadside verges, using coarse, infertile soil as roadfill to create a poor seedbed for exotic species, building roads through more-resistant community types, and reestablishing native vegetation along roads after construction (Bugg et al. 1997). Road-maintenance measures such as mowing, grading, and herbicide application should be timed carefully to maximize their detrimental effects on exotic plants and minimize those on native plants (Benefield et al. 1999).

Management efforts to prevent or slow the spread of exotic plants into and away from roadsides should include preventing and minimizing soil-surface disturbance in interior habitats adjacent to roads (e.g., Belnap et al. 2001) and must recognize that communities characterized by high resource availability (i.e., deep, silty, or otherwise fertile soils) are particularly vulnerable to disturbance and invasion. It would also be helpful if data on exotic plants were collected during roadside maintenance and weed-control efforts to monitor the effects of different management strategies on exotic plant invasions. This would allow for adaptive management in which roadside-maintenance activities could be experimentally manipulated to work toward decreasing both the susceptibility of roadside habitats to invasion and the likelihood that roadside invasions will spread into adjacent natural ecosystems.

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