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Native weeds and exotic plants: relationships to disturbance in mixed-grass prairie*

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Abstract

Disturbance frequently is implicated in the spread of invasive exotic plants. Disturbances may be broadly categorized as endogenous (e.g., digging by fossorial animals) or exogenous (e.g., construction and maintenance of roads and trails), just as weedy species may be native or exotic in origin. The objective of this study was to characterize and compare exotic and native weedy plant occurrence in and near three classes of disturbance – digging by prairie dogs (an endogenous disturbance to which native plants have had the opportunity to adapt), paved or gravel roads (an exogenous disturbance without natural precedent), and constructed trails (an exogenous disturbance with a natural precedent in trails created by movement of large mammals) – in three geographically separate national park units. I used plant survey data from the North and South Units of Theodore Roosevelt National Park and Wind Cave National Park in the northern mixed-grass prairie of western North and South Dakota, USA, to characterize the distribution of weedy native and exotic plants with respect to the three disturbance classes as well as areas adjacent to them. There were differences both in the susceptibility of the disturbance classes to invasion and in the distributions of native weeds and exotic species among the disturbance classes. Both exotic and native weedy species richness were greatest in prairie dog towns and community composition there differed most from undisturbed areas. Exotic species were more likely to thrive near roadways, where native weedy species were infrequently encountered. Exotic species were more likely to have spread beyond the disturbed areas into native prairie than were weedy native species. The response of individual exotic plant species to the three types of disturbance was less consistent than that of native weedy species across the three park units.

Introduction

Disturbance is widely recognized as a primary influence on plant community composition and is frequently implicated in the spread of invasive exotic plants (Hobbs and Humphries 1995). A variety of plant life-history characteristics are associated with an ability to exploit disturbances (Rejmanek 1996). Some of these characteristics contribute to weediness in plants (Baker 1974), regardless of whether species are native to an area or exotic introductions.

Disturbance itself typically results in reversion to an earlier stage of plant succession. Pickett and White (1985) have defined disturbance as "...any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." Some disturbances have an evolutionary history, such that a community of plants may exist in association with that disturbance. These have been termed indigenous (Denslow 1985) or endogenous (Fox and Fox 1986) disturbances, examples of which include digging by fossorial mammals such as badgers (*Taxidea taxus*) and prairie dogs (*Cynomys* spp.) in grasslands, gap creation by windfall in forested en-

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vironments, and periodic flooding of riparian zones. Another category of disturbances is of more recent origin; these disturbances are associated with human activities that have accelerated dramatically in the last several centuries, such as road building, creation of urban centers, and large-scale agriculture [i.e., exotic (Denslow 1985) or exogenous (Fox and Fox 1986) disturbances].

If both endogenous and exogenous disturbances involve similar processes, we can expect that plant species evolutionarily adapted to exploitation of disturbed habitats should thrive in either. Similarly, if introduced species are functionally similar to native species that depend on disturbance, we should find similar responses between weedy native and exotic plant species to either endogenous or exotic disturbance. In this study, I use plant survey data from three geographically separate national park units in the northern mixed-grass prairie of western North and South Dakota, USA, to characterize the response of weedy native and exotic plants to three types of disturbance present in each park unit. One of these disturbances, digging by fossorial mammals, has a long evolutionary history in mixed-grass prairie. The other two, constructed trails and roadways and their associated traffic and maintenance, are of recent origin, but different intensities.

Black-tailed prairie dogs (*Cynomys ludovicianus*) are long-standing inhabitants of the northern Great Plains (Goodwin 1995) and their effects on soil and vegetation constitute a disturbance regime to which native plants have had the opportunity to adapt (Koford 1958; Detling 1998). Burrowing activity changes soil characteristics, mixes layers of soil, and brings soils and seeds from deeper layers to the surface (Kotliar et al. 1999). Prairie dog grazing changes both the structure and species composition of the vegetation and influences its nutrient content (Coppock and Detling 1986; Holland et al. 1992; Detling 1998, 1998). Larger herbivores are attracted to more nutritious forage on prairie dog colonies, further contributing to soil and vegetation disturbance and propagule input (Coppock et al. 1983b).

Constructed hiking trails, although recent in origin, have precedent in trails created by habitual movements of large mammals. The sorts of disturbance associated with both constructed and "natural" trails include soil compaction and erosion, disruption of the vegetative canopy, removal of litter, and enhanced nutrient and propagule input through livestock and wild mammal dung (Bright 1986; Hall and Kuss

1989; Adkison and Jackson 1996; Deluca et al. 1998). Constructed trails differ somewhat from natural trails in that features often are built to direct water off the trail during heavy rainfall; vegetation is periodically cut back from the trail; and livestock (mainly horses, but increasingly other species) from substantial distances may be brought in for packing and trail rides, thus potentially introducing seed from species, cultivars and genotypes not present in the park.

Roads have no naturally occurring analogues. Their construction may involve wholesale movement and compaction of soil; application of impermeable pavement that changes both runoff and soil characteristics; introduction of a new seedbank, often composed of exotic species, to stabilize roadside soils; and continued propagule, nutrient, and pollutant input from traffic on the road (Knops et al. 1995; Greenberg et al. 1997; Forman and Alexander 1998; Forman 2000; Forman and Deblinger 2000; Parendes and Jones 2000; Trombulak and Frissell 2000). Roadside maintenance typically includes periodic mowing and herbicide applications for noxious weed control (Forman and Alexander 1998). In this study, I did not distinguish between gravel and paved roads.

In terms of the disturbance regime descriptors in White and Pickett (1985), the three disturbances vary in terms of distribution, frequency, and severity. Prairie dog towns, because of their biotic origin, tend to occur in similar landscape positions, while roads and trails are linear features that traverse many different landscapes and vegetation types. Disturbance on prairie dog towns is nearly continuous with respect to the growing season of the vegetation. Roadside maintenance is more episodic, with mowing and spraying frequencies of once to several times per season, although traffic effects are continuous. Trail use and maintenance varies; the most accessible sections of trails receive continual use through the growing season but maintenance occurs only at multi-year intervals on all trails. Roads exhibit the most severe disturbance, in that vegetation is completely removed both from the roadbed and from some distance on either side. Prairie dog towns represent somewhat less severe disturbance, with the vegetation gradually replaced over time as the colony expands. Trails represent the least severe disturbance, in that only the trailbed itself is kept free of vegetation.

The objective of this study was to characterize and compare exotic and native weedy plant occurrence in and near these three classes of disturbance in three national park units. In particular, I asked (1) do ex-

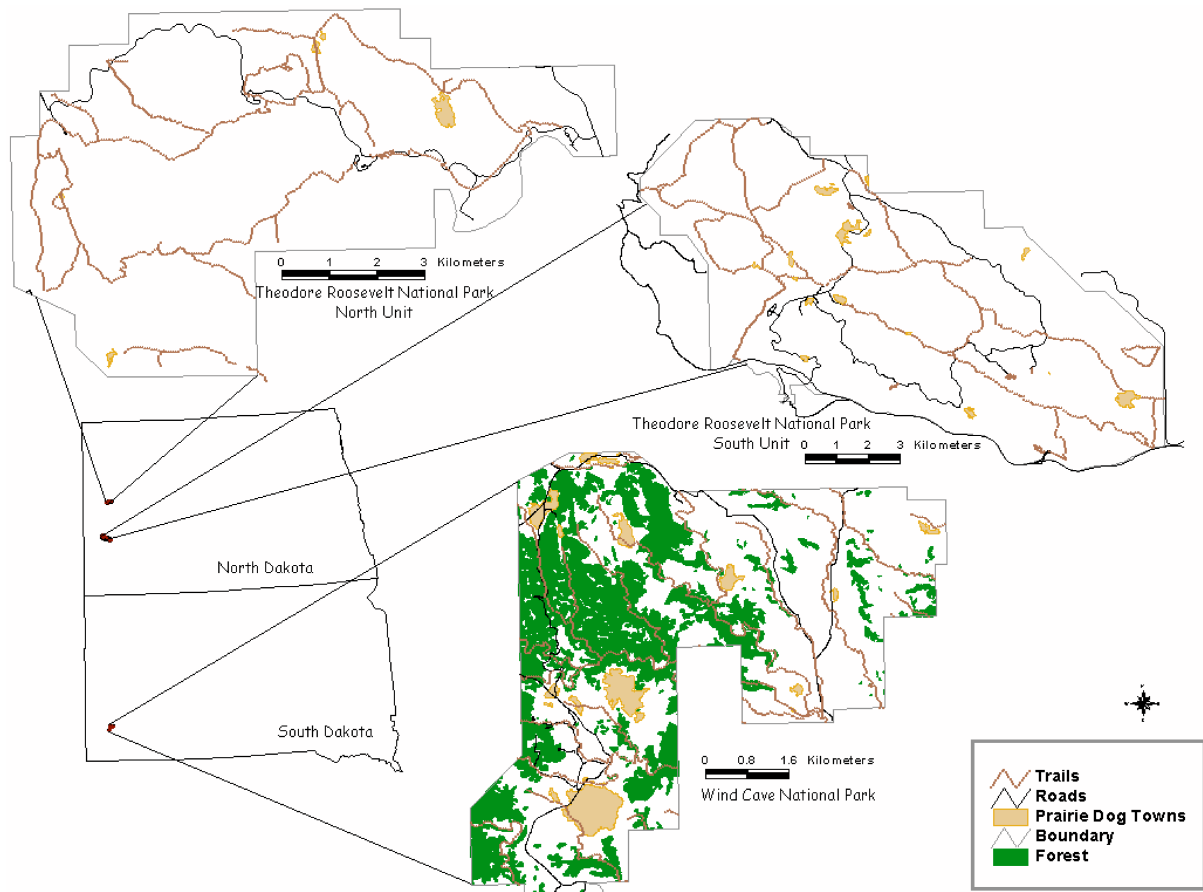


Figure 1. Location of study sites in North Dakota and South Dakota, USA.

otic and native weedy species vary in terms of species richness and plant community composition among disturbance classes; (2) are species consistent in their exploitation of different disturbance classes across geographically separate park units; and (3) do exotic and native weedy species differ in the extent to which they colonize areas adjacent to disturbance? My goals were to gain insight into ways that native and exotic plants differ in their exploitation of disturbance and the ways that disturbances vary in their invasibility.

Methods

Study areas

The study was conducted in three national park units within the northern mixed-grass prairie (Figure 1). Theodore Roosevelt National Park (TRNP) in west-

ern North Dakota, USA, consists of two units separated by roughly 115 km of federally and privately owned rangeland. The south (TRSU) and north (TRNU) units of the park comprise approximately 18,600 and 9,600 ha, respectively. The landscape is dissected by badlands and the Little Missouri River flows through both park units. Vegetation is mixed-grass prairie throughout. TRNU has approximately 26 km of roads and 53 km of constructed and maintained trails (hereafter trails); TRSU has 56 and 97 km of roads and trails, respectively. The two units were designated a national park in 1947 (TRSU) and 1948 (TRNU). Twenty-three native vegetation types in the two park units have been delineated on a geographic information system (GIS; TRNP, unpublished**).

Wind Cave National Park (WCNP) is located in western South Dakota near the southeastern edge of

** These maps may be viewed or downloaded in Arc/Info Exchange Format from [http://www.nps.gov/gis/midwest_data.html#North Dakota](http://www.nps.gov/gis/midwest_data.html#North%20Dakota).

the Black Hills. WCNP comprises approximately 11,355 ha, 75% of which is mixed-grass prairie. The remainder is dominated by pine forest (*Pinus ponderosa*) and was excluded from the current analysis. The park was established in 1903 although it did not achieve its current size until 1946, at which time bison, elk, and pronghorn were released from enclosures to roam freely through the park. WCNP has approximately 55 km of roads and 49 km of trails.

All three park units have fenced perimeters and are home to free-roaming bison, pronghorn, elk and deer. Feral horses also are present in TRSU. Pack animals are allowed on trails at TRNP but not at WCNP. Human visitation rates vary widely among the three park units, with 14,326, 44,749 and 320,915 vehicles entering TRNU, TRSU and WCNP, respectively, in 2000. Backcountry permits issued, an indication of visitor use of trails, more closely approximated the relative extent of the trail system in the three park units; 310, 661 and 245 permits were issued at TRNU, TRSU and WCNP in 2000, respectively.

Vegetation sampling

Details of the vegetation sampling design for TRNP have been presented elsewhere (Larson et al. 2001); with a few exceptions, similar methods were used to survey WCNP. To summarize briefly, I divided WCNP and both units of TRNP into rectangular strata, roughly 800 ha each. Using GIS maps, I randomly selected three points in each vegetation type in each stratum at TRNP and recorded the coordinates so they could be located with Global Positioning System (GPS) units in the field. Because there was no vegetation map for WCNP at the time, I used an elevation contour map to divide the landscape into five terrain classes: steep slope, gentle slope, ridge top, swale, or flat. In both parks, transects were oriented perpendicular to elevation contour lines, starting at the edge of the vegetation type or terrain type and passing through the randomly generated point. Allocation of plots (0.5 × 2.0 m) on each transect was proportional to the square root of the area of the vegetation or terrain type within the stratum. However, for purposes of this analysis, I used only the first four plots on each transect to avoid problems of unequal sampling effort among the disturbance classes, which were independent of vegetation and terrain types. Plots were oriented parallel to elevation contour lines and field personnel recorded presence of all species that occurred in each plot. Occurrences were summed

over each transect to determine frequency of each plant species on each transect.

Although it would have been desirable to sample in each park unit each year in a random fashion, for logistical reasons TRSU was surveyed in 1996, TRNU in 1997, and WCNP in 1998. Of the species encountered, yearly changes in population size are likely to be important in *Melilotus officinalis*, a biennial known to show strong year-to-year fluctuations (Turkington et al. 1978), and in annual species whose abundances may fluctuate in response to climatic variability. For most species, sampling of species frequency rather than cover minimizes differences associated with seasonal and yearly fluctuations (Elzinga et al. 1998). Vegetation was sampled once between 15 May and 31 September each year. Taxonomy follows Barker et al. (1986).

I classified transects *a posteriori* into one of eight disturbance classes, (1) within a prairie dog town, (2) between the edge of a prairie dog town and 100 m from the edge, (3) between 100 and 200 m from the edge of a prairie dog town, (4) within 100 m of the edge of a road, (5) between 100 and 200 m of the edge of a road, (6) within 100 m of a trail, (7) between 100 and 200 m of a trail, or (8) > 200 m from any prairie dog town, road, trail, and other known disturbance. I included all trails constructed and maintained by the parks, although the level of use and maintenance of individual trails was not quantified. All roads with a gravel or paved surface were included in the study. A few transects fell into more than one category and were excluded from this analysis because of the small sample size for these combined categories. Note that the only disturbance class completely restricted to the disturbance itself is within prairie dog towns. The classes that included transects within 100 m of roads and trails include not only the edge of the road or trail, but 100 m on either side and transects did not always cross the road or trail. Thus, the < 100 m from road and < 100 m from trail classes are best thought of as prairies adjacent to the disturbance. I chose 100 m as the cutoff for the classes adjacent to disturbance because Forman (2000) found that the ecological influence of roadways extended at least 100 m from the edge of the blacktop. Those classes between 100 and 200 m of a disturbance were included to ascertain that effects had indeed diminished by that point. This sampling design resulted in 454 transects in TRNU, 800 in TRSU and 178 in WCNP.

I used Barker et al. (1986) to classify species as alien or native, and to further classify native species as weedy or not weedy. Any native species described as weedy, or as inhabiting primarily waste places or disturbed areas, irrespective of my observations at the parks, was considered weedy for purposes of this analysis. This definition of weedy corresponds to Rejmanek (1995) "colonizer."

Statistical analysis

Two analyses were performed and each was done separately on exotic and native weedy species at each park unit. First, I performed a one-way analysis of variance (ANOVA) to determine if mean number of species/transect varied among disturbance types. I tested the hypothesis that means on transects in each disturbance class differed from the mean on transects > 200 m from any known disturbance via Fisher's LSD test (Milliken and Johnson 1984). This comparison implicitly recognizes that areas not subject to the kinds of disturbance considered in this analysis are not free of disturbance, and thus reflect background levels of disturbance and invasibility. Second, I did a canonical discriminant analysis (CDA) (SAS Institute, Inc. 1999) to assess the relative importance of the disturbance classes in the distribution of the exotic and weedy native species. A stepwise discriminant analysis [PROC STEPDISC; (SAS Institute, Inc. 1999)] was first performed on each data set to select relevant species for the CDA. I obtained disturbance class means for each significant canonical variate. Individual species' frequencies were correlated with the canonical variates using Pearson product-moment correlation. As part of the CDA, Mahalanobis distances were calculated between plant communities in each disturbance class (including > 200 m from any known disturbance). The squared Mahalanobis distance from i to j is defined as

$$D^2(i;j) = (\bar{X}_i - \bar{X}_j)' COV^{-1} (\bar{X}_i - \bar{X}_j)$$

where COV is the pooled covariance matrix and X is the vector containing the quantitative variables.

F-tests were used to determine which communities differed from one another with respect to Mahalanobis distances. Statistical significance was set at $p \leq 0.05$. Note that because all species were not present in all disturbance classes, the data cannot be made multivariate normal, so p values for the CDAs, which are in this case descriptive (Khattree and Naik (2000),

p 282–283), should be regarded as an index of fit *sensu* Mitchell (1993) rather than a level of significance for formal hypothesis testing.

Results

All native weedy and exotic species found in the parks, along with the proportion of transects on which they occurred in each disturbance class in each park unit, can be found in Appendix 1. The stepwise discriminant analysis identified 13 native and 19 exotic species at TRNU, 7 native and 16 exotic at TRSU, and 9 native and 8 exotic at WCNP that best discriminated among the disturbance classes (see Appendix 1 for identities of species chosen).

Native weedy species richness was greatest within prairie dog towns in all three park units (Figure 2) and their communities were most different from other disturbance class communities (Figure 3, Table 1). The first canonical variate at each park unit was associated with vegetation within prairie dog towns, and accounted for 91, 99 and 90 percent of native weedy species variation at TRNU, TRSU, and WCNP, respectively. Native weedy communities within prairie dog towns varied significantly, as indicated by Mahalanobis distances, not only from undisturbed areas, but from all other disturbance types at all three park units (Table 1). The native weedy communities in most other disturbance classes were similar to one another (Figure 3, Table 1). At WCNP and TRSU, native weedy communities within prairie dog towns were the only ones to vary from other native weedy communities. At TRNU, however, native weedy communities within 100–200 m of prairie dog towns also differed from all others, but those < 100 m from prairie dog towns generally did not (Table 1). The overall anova for native weedy species richness indicated significant differences in each park unit ($P < 0.0001$ in each case). Native weedy species richness was never elevated near roads or trails, although native weedy species richness at WCNP was significantly lower within 100 m of roads than on undisturbed transects (Figure 2). Native weedy species were not characteristic of transects within 100 m of prairie dog towns, although a distinctive community of native weeds, primarily characterized by the presence of *Gutierrezia sarothrae* (Table 2), existed 100–200 m from prairie dog towns at TRNU (Figure 3). This association represented the only other significant canonical variate for native weedy species and accounted for only

5 percent of their variation at TRNU. All of the correlations between native weedy species and CV1 were positive, and half of the native weedy species considered in the analysis were significantly correlated with this variate in more than one park unit (Table 2).

Exotic species also were most diverse (Figure 2; overall ANOVA $p < 0.0001$ for each park unit) and their communities most distinctive (Figure 3, Table 1) in prairie dog towns, but unlike native weedy species, exotic species also were characteristic of areas within 100 m of roads or prairie dog towns, and species richness was elevated within 100 m of trails, in one or more park units (Figure 2). Again, the first canonical variate represented vegetation within prairie dog towns and accounted for 88, 86, and 73 percent of exotic species variation at TRNU, TRSU and WCNP, respectively. Even though the first variate represented the same disturbance type in each park unit, only five of the 18 exotic species associated with this variate had a positive correlation with it in more than one park unit (Table 3). Note that all but one of these 18 species occurred in more than one unit (Appendix 1). Unlike native weedy species, where all associations within prairie dog towns were positive (Table 2), two exotic species, *Euphorbia esula* and *Poa pratensis*, were each negatively correlated with this disturbance class in one park unit (Table 3).

The CDA for exotic species revealed a second significant canonical variate at all three park units (marginally so at WCNP), but the variate was correlated with different disturbance classes at each unit. At TRNU, the second variate, which accounted for 7% of exotic species variance, separated vegetation within 100 m of prairie dog towns from all other disturbance classes (Figure 3) and was characterized by *Bromus japonicus* and *Cirsium arvense* (Table 3). The second variate at TRSU represented roadside vegetation, was strongly dominated by *Bromus inermis* (Table 3), and accounted for 7% of the variance in exotic species. A third variate also was significant at TRSU but accounted for only 3% of exotic species variance; it represented vegetation within 100 m of prairie dog towns (Figure 3) and was characterized by positive associations with *Medicago sativa*, *Convolvulus arvensis*, and *Camelina microcarpa* (Table 3). The second canonical variate at WCNP separated vegetation 100–200 m from roads from all others (Figure 3) and accounted for 14% of the variation in exotic species at that park. *Cynoglossum officinale* was most strongly correlated with that variate, and *Poa pratensis*

and *Tragopogon dubius* somewhat less so (Table 3).

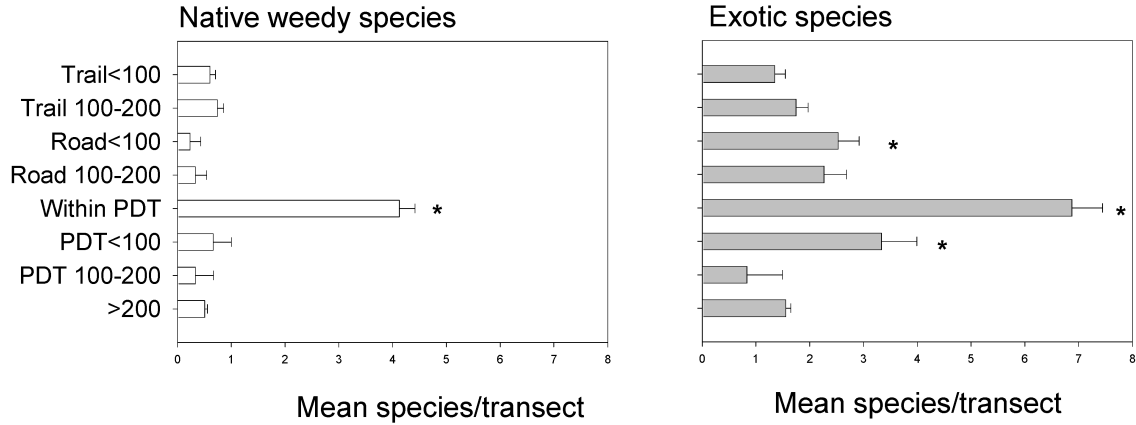
Discussion

Exotic and native weedy species differed in their exploitation of exotic and endogenous disturbance, as demonstrated by their frequencies and distributions in prairie dog towns and along roads and trails. Prairie dog towns, reflecting endogenous and continuous disturbance, were exploited by both exotic and native weedy plant species (Figures 2 and 3). Roadways, an exogenous, severe and episodic disturbance, provided habitat for exotic, but not native, weeds. In general, neither native weeds nor exotic species were associated with trails (Figures 2 and 3), where disturbance is less frequent and less severe. Exotic species invaded areas adjacent to prairie dog disturbances and created exotic communities that were distinct from those in either undisturbed areas or within prairie dog towns; native weeds did not (Figures 2 and 3). Thus, the disturbance classes varied in overall susceptibility to invasion and exotic and native weedy community composition varied among disturbance classes.

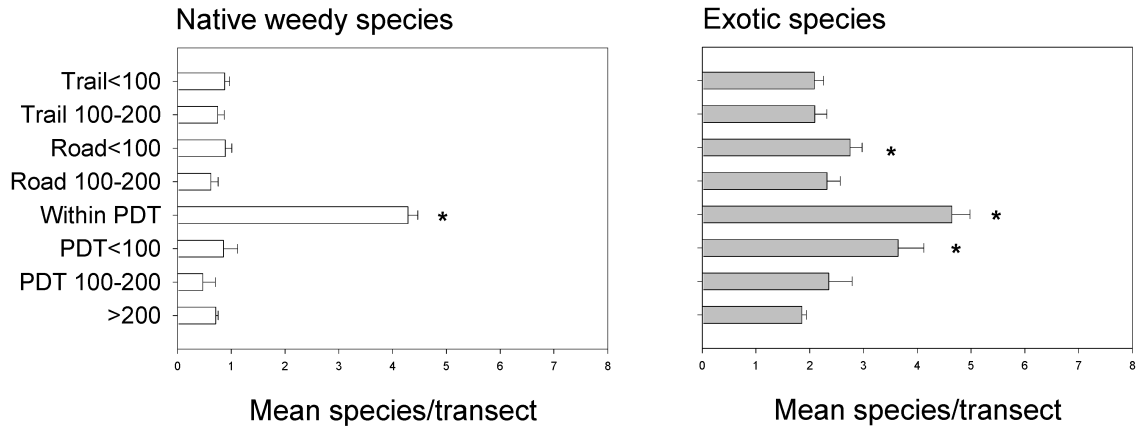
Comparison of disturbance classes

Prairie dog towns provided habitat for most of the species considered in this study (Tables 2 and 3). In most cases, it can be inferred that prairie dogs themselves, and other herbivores attracted to the towns, played a role in species composition within the towns. Of the natives, only *Gutierrezia sarothrae*, a perennial subshrub, failed to be associated with the interior of prairie dog towns (Table 2). Bonham and Lerwick (1976) attributed the absence of *G. sarothrae* from prairie dog towns in shortgrass steppe in Colorado to selection for shorter stature vegetation imposed by prairie dogs, which clip vegetation to a few centimeters in height within their colonies (Koford 1958). Five of the exotic species showed no relationship to the interior of prairie dog towns (Table 3). Of these, *Medicago sativa*, a perennial legume, and *Camelina microcarpa*, an annual mustard, were associated with areas within 100 m of dog towns at TRSU, despite their lack of association with the interior. This pattern may suggest active exclusion by prairie dogs: both species take advantage of disturbed soil and would be expected within the towns unless they were actively excluded. *Bromus inermis* was strongly associated

Theodore Roosevelt National Park, North Unit



Theodore Roosevelt National Park, South Unit



Wind Cave National Park

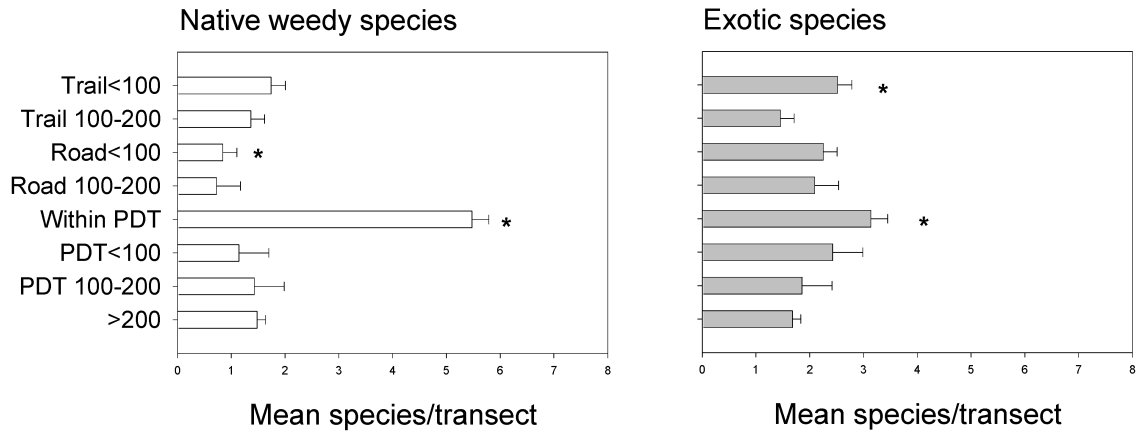


Figure 2. Mean number of species encountered on transects located in each disturbance class. Asterisks denote means that are significantly different from undisturbed (> 200) transects.

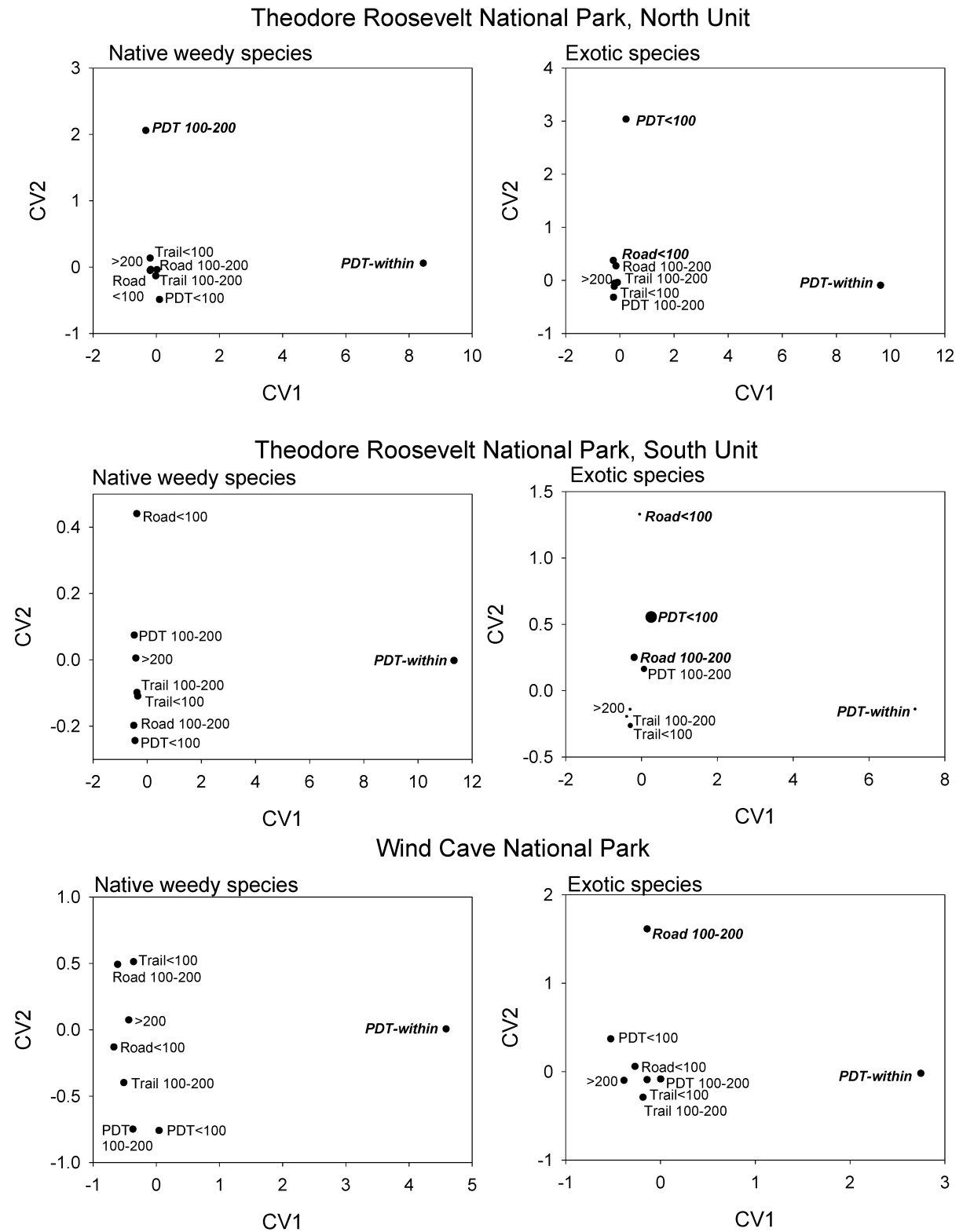


Figure 3. Class means for canonical variables. Labels in bold italicized represent means that are significantly different from the undisturbed class. CV2 was not statistically significant for native weedy species at TRSU or WCNP, but was plotted for consistency. CV3 was significant for exotic species at TRSU and is reflected in the size of the dots on the graph.

Table 1. Squared Mahalanobis distances between disturbance types. Higher values imply greater differences in plant communities between the two types. Because values are dependent on sample size, the magnitudes are not comparable among comparisons. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

	> 200	PDT 100–200	PDT < 100	Within PDT	Road 100–200	Road < 100	Trail 100–200	n
Theodore Roosevelt National Park, North Unit – native weedy species								
> 200	–							285
PDT 100–200	4.60***	–						6
PDT < 100	2.29	7.74**	–					6
Within PDT	74.46***	81.36***	72.13***	–				8
Road 100–200	0.73	5.62**	3.69*	71.79***	–			15
Road < 100	0.07	4.90**	2.86	74.88***	0.52	–		17
Trail 100–200	0.08	5.08***	2.17	71.82***	0.36	0.18	–	51
Trail < 100	0.07	4.07**	2.85*	74.80***	0.73	0.05	0.19	66
Theodore Roosevelt National Park, North Unit – exotic species								
> 200	–							285
PDT 100–200	0.12	–						6
PDT < 100	10.03***	11.69***	–					6
Within PDT	96.29***	97.41***	98.49***	–				8
Road 100–200	0.63	1.12	9.26***	96.02***	–			15
Road < 100	1.49**	2.06	10.11***	98.74***	0.52	–		17
Trail 100–200	0.10	0.35	10.19***	94.45***	0.36	1.15	–	51
Trail < 100	0.06	0.12	10.38***	96.72***	0.73	1.72**	0.22	66
Theodore Roosevelt National Park, South Unit – native weedy species								
> 200	–							453
PDT 100–200	0.03	–						17
PDT < 100	0.47	0.63	–					14
Within PDT	138.09***	139.42***	139.29***	–				28
Road 100–200	0.16	0.22	0.26	139.93***	–			53
Road < 100	0.24	0.25	0.70	137.47***	0.48	–		64
Trail 100–200	0.03	0.12	0.35	137.13***	0.12	0.31	–	64
Trail < 100	0.07	0.15	0.47	136.46***	0.25	0.37*	0.04	107
Theodore Roosevelt National Park, South Unit – exotic species								
> 200	–							453
PDT 100–200	1.22	–						17
PDT < 100	5.29***	5.27*	–					14
Within PDT	61.94***	57.94***	58.93***	–				28
Road 100–200	0.61*	1.54	5.85***	61.00***	–			53
Road < 100	2.35***	2.53*	5.89***	59.12***	1.83***	–		64
Trail 100–200	0.23	1.69	5.34***	63.67***	0.83	2.76***	–	64
Trail < 100	0.20	1.11	5.28***	62.15***	0.85*	2.85***	0.36	107
Wind Cave National Park – native weedy species								
> 200	–							87
PDT 100–200	1.41	–						7
PDT < 100	1.86	2.35	–					7
Within PDT	25.27***	25.90***	22.20***	–				21
Road 100–200	0.67	2.76	3.04	27.59***	–			11
Road < 100	0.52	1.98	2.24	27.90***	0.78	–		32
Trail 100–200	0.30	0.81	1.65	26.23***	1.27	0.49	–	33
Trail < 100	0.33	2.14	2.67	24.84***	0.66	1.03	0.95	31
Wind Cave National Park – exotic species								
> 200	–							87
PDT 100–200	0.74	–						7
PDT < 100	1.20	1.25	–					7
Within PDT	9.84***	7.98***	11.63***	–				21
Road 100–200	3.12***	3.68	3.22	11.15***	–			11
Road < 100	0.16	0.32	0.74	9.16***	2.72**	–		32
Trail 100–200	0.39	1.13	2.44	8.99***	3.68***	0.63	–	33
Trail < 100	0.53	0.20	0.63	8.66***	3.67***	0.19	1.08*	31

Table 2. Correlation coefficients between native weedy species and canonical variates in each park unit. Only significant ($p < 0.05$) correlations and variates are shown; the p value associated with the variate is shown beneath each park unit acronym. The disturbance class correlated with the variate is shown beneath the variate.

Species	CV1 Within PDT		CV2 PDT 100–200	
	TRNU ($p < 0.0001$)	TRSU ($p < 0.0001$)	WCNP ($p < 0.0001$)	TRNU ($p < 0.0149$)
<i>Aristida purpurea</i>			0.51	
<i>Asclepias verticillata</i>		0.21	0.57	
<i>Collomia linearis</i>	0.37			
<i>Conyza canadensis</i>	0.45	0.39		-0.20
<i>Dyssodia papposa</i>		0.98		
<i>Euphorbia glyptosperma</i>			0.59	
<i>Euphorbia spathulata</i>	0.40			
<i>Gutierrezia sarothrae</i>				0.96
<i>Hedeoma hispidum</i>			0.57	
<i>Lepidium densiflorum</i>	0.57	0.19		
<i>Oxalis stricta</i>	0.76		0.77	
<i>Schedonnardus paniculatus</i>	0.46	0.66	0.85	

with roadsides at TRSU (Table 3), having been planted there for stabilization. Despite the fact that roads at TRSU frequently bisect prairie dog towns (Figure 1), the grass has not spread into the towns, again suggesting exclusion by prairie dogs. Although relatively abundant in each park unit (Appendix 1), *Tragopogon dubius* was associated only with transects 100–200 m from roads at WCNP (Table 3). The absence of *T. dubius* from prairie dog towns may be explained by palatability of both above- and belowground portions of the plant (Reichman and Smith 1991).

Two exotic species were weakly negatively associated with prairie dog towns, *Euphorbia esula* at TRSU and *Poa pratensis* at WCNP (Table 3). Larson et al. (2001) found that *E. esula* frequency tended to be associated with mesic native vegetation types at TRSU. Prairie dog towns occupy topographic positions that rarely intersect these vegetation types. At WCNP, *P. pratensis* follows the pattern of most native perennial grasses, in that they tend to decline on prairie dog towns compared with uncolonized mixed-grass prairie (Coppock et al. 1983a).

Together, these examples emphasize the point made by many others (Coppock et al. 1983b; Weltzin et al. 1997; Detling 1998, 1998) that prairie dogs influence vegetation beyond the simple act of creating soil disturbance. The exclusion of many of the species that were not associated with prairie dog towns likely resulted from direct effects of prairie dogs and other herbivores, rather than an inability on the part

of the plant species to take advantage of soil disturbance. That most native weedy species were associated with prairie dog towns is hardly surprising. Not only were prairie dog towns one of the most widespread disturbances during the evolutionary history of the Great Plains (Goodwin 1995), but the presence of certain plant species in such locations likely influenced their classification as weedy in references such as Barker et al. (1986).

Roads have often been characterized as conduits for dispersal of exotic plants (Greenberg et al. 1997; Parendes and Jones 2000; Trombulak and Frissell 2000). The current study lends support to this observation, but also raises a question: Why are the 100 m on either side of a road not equally invaded by both exotics and native weedy species? The implication is that roadsides constitute a substantively different type of disturbance than native weeds evolved to exploit. Roadsides are often densely planted with aggressive sod-forming grasses, which result in closed canopies and few opportunities for seedling establishment. Disturbance caused by prairie dogs, on the other hand, results in canopy opening and a more conducive environment for seedling establishment. Prairie dogs also enhance the soil nutrient environment (Coppock et al. 1983b), and experimental work (Hobbs and Atkins 1988; Burke and Grime 1996) has shown that the combination of soil disturbance and nutrient addition facilitates invasion over either factor alone.

Kotanen et al. (1998) observed that the capacity to exploit riparian, roadside and undisturbed grasslands

in shortgrass steppe in Colorado separated exotic and native taxa, which the authors suggested was in part a result of favorable soil moisture along roadways. Likewise, McIntyre and Lavorel (1994a, 1994b) concluded that moisture enrichment along roadways favored exotic species in relatively dry grasslands of Australia. Such increased moisture also may have favored exotic plants along roads at TRNP. The lack of such an effect at WCNP may reflect generally greater moisture availability at that park; the year in which vegetation was sampled at WCNP was the third year in a row in which precipitation at the site exceeded the 30-year mean by > 12.7 cm (National Climate Data Center; <http://lwf.ncdc.noaa.gov/oa/climate/stationlocator.html>). In contrast, both units of TRNP had near – normal precipitation during the same period.

Trails also have been considered to be avenues of dispersal for invasive species (Benninger et al. 1992; Tyser and Worley 1992). This did not seem to be the case in the present study. Although exotic species richness was greater within 100 m of trails at WCNP (Figure 2), species composition did not vary significantly from undisturbed transects for either exotic or native weedy species, nor did trailside vegetation differ from undisturbed at WCNP or at any other park unit (Table 1).

Consistency across park units

If species respond to disturbances in a consistent manner in different geographic areas, it then becomes possible to make predictions regarding new infestations. Because of their overwhelming association with prairie dog towns (Table 1, Figures 2 and 3), native weedy species' distributions with respect to the disturbance classes considered here were quite similar from one park unit to another. Exotics were far less restricted in the disturbance classes they exploited (Figure 3) and often failed to be significantly associated with the same disturbance classes in different parks (Table 3). The implication is that those exotic species that tend to be restricted to prairie dog towns across all park units may be expected to behave in ways similar to native weedy species, and thus are less likely to constitute a threat to undisturbed native prairie. Conversely, those exotics that exploit different disturbances in different parks, or that have distributions unrelated to disturbance, require greater surveillance, since their behavior is less predictable as well as less similar to the native weeds that do not invade undisturbed prairie.

Distribution outside of disturbances

Species characteristic of areas adjacent to disturbances might be considered more likely to invade native prairie than those species confined to the disturbance itself. Axes in CDAs at two park units (TRNU and TRSU) separated exotic species within 100 m of prairie dog towns from other disturbance classes, as well as from undisturbed transects (Table 1, Figure 3). It could be argued that no area is disturbance-free, and especially one so near to a heavily disturbed area. However, the question remains as to why only exotic species and not native weedy species characterized this area. If proximity to propagules provided the answer, one would expect native weedy species also to colonize areas adjacent to prairie dog towns, and this was not the case (Table 1).

Thompson et al. (1995) analyzed characteristics of native and alien invasive plants in the Netherlands, England, Scotland and Ireland and concluded that the greatest functional differences lie between invasive and non-invasive species, rather than between aliens and natives. Of the exotic species at TRNU, two annual grasses (*Bromus japonicus* and *B. tectorum*), one annual mustard (*Thlaspi arvense*), one perennial grass (*Poa pratensis*) and two perennial forbs (*Cirsium arvense* and *Convolvulus arvensis*) were characteristic both of transects within and adjacent to prairie dog towns (Table 3). All of these species have been considered invasive under some circumstances (Weaver and Riley 1982; Evans 1984; Stubbendieck et al. 1994; Knapp 1996; Haferkamp et al. 1997) and some are serious agricultural pests. By contrast, the native weedy species in this study are generally considered invasive only in an agricultural context (e.g., see Stubbendieck et al. (1994)). Daehler (1998) noted that, globally, those families that were over-represented among agricultural weeds but not among natural area invaders contained many ruderal species. All of the native weedy species in the present study would be considered ruderal. At least three of these species, *Ambrosia psilostachya*, *Conyza canadensis* and *Panicum capillare*, have been carried to continents outside North America, yet apparently only exploit disturbed soils and do not invade natural areas (Dafni and Heller 1990; Guillerme et al. 1990; Rich 1994; Thebaud et al. 1996).

This study provides little evidence for effects of the three disturbance classes beyond 100 m. In the two cases in which Mahalanobis distance indicated a significant difference between communities at 100–

200 m and those in undisturbed areas, such differences were not found at < 100 m (Table 1). Lacking a probable mechanism to explain such a leap, a more likely explanation involves the stochastic nature of disturbances on the landscape along with native vegetation types that favor some species over others. These variables were not taken into account in this analysis, but nonetheless are important contributors to plant species distribution in these prairies (Larson et al. 2001).

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Appendix

Table A1. Proportion of transects upon which at least one individual of the species occurred in each park unit. Species are alphabetical by genus. Bold park unit acronyms indicate that the species was identified in the stepwise discriminant analysis as influential in distinguishing among the disturbance classes at that park unit; these species were used in the canonical discriminant analysis.

Species	Unit	PDT		PDT		Road	Road	Trail	Trail
		> 200	100–200	< 100	within	100–200	< 100	100–200	< 100
Native species									
<i>Ambrosia psilostachya</i>	TRNU	0.13	0	0	0	0	0	0.14	0.08
	TRSU	0.02	0	0.07	0.04	0.06	0.03	0.03	0.01
	WCNP	0.17	0.14	0.1	0.14	0	0.18	0.13	0.09
<i>Aristida purpurea</i>	TRSU	0.06	0	0	0.04	0	0.02	0.06	0.07
	WCNP	0.32	0.14	0.67	0.43	0.19	0	0.32	0.33
<i>Asclepias verticillata</i>	TRNU	0	0	0	0	0	0	0.02	0.03
	TRSU	0.01	0	0	0.14	0	0	0.02	0.01
	WCNP	0.17	0.14	0.67	0.14	0.03	0	0.1	0.18
<i>Cirsium flodmanii</i>	TRSU	0	0.06	0	0.07	0	0	0	0.01
	WCNP	0	0	0	0	0	0	0	0
<i>Collomia linearis</i>	TRNU	0.02	0	0	0.38	0.07	0	0.02	0
	TRSU	0.08	0	0	0.11	0.06	0.06	0.09	0.07
	WCNP	0.02	0.14	0.14	0	0.09	0	0.06	0.03
<i>Conyza canadensis</i>	TRNU	0.03	0	0.33	0.5	0	0	0.04	0
	TRSU	0.02	0	0	0.39	0.02	0.02	0.05	0.05
	WCNP	0.13	0	0.43	0.14	0.03	0	0.06	0.06
<i>Dyssodia papposa</i>	TRSU	0	0	0	0.93	0	0.02	0	0
	WCNP	0	0	0.19	0	0	0	0	0
<i>Euphorbia glyptosperma</i>	TRSU	0.02	0.06	0	0.21	0.02	0.03	0.03	0.03
	WCNP	0.05	0.14	0.38	0.14	0	0	0.1	0
<i>Euphorbia spathulata</i>	TRNU	0.01	0	0	0.5	0.13	0.06	0.06	0.05
	TRSU	0.07	0.06	0.07	0.11	0.08	0.13	0.06	0.12
	WCNP	0.02	0	0.1	0	0.06	0.09	0.1	0
<i>Grindelia squarrosa</i>	TRNU	0.04	0	0	0	0	0	0.08	0.11

Table A1. Continued.

Species	Unit	PDT		PDT		Road		Trail	
		> 200	100–200	< 100	within	100–200	< 100	100–200	< 100
<i>Gutierrezia sarothrae</i>	TRSU	0.07	0	0.14	0.04	0.02	0.06	0.09	0.06
	WCNP	0.02	0	0	0	0	0	0	0.03
	TRNU	0.01	0.17	0	0	0	0	0	0.02
<i>Hedeoma hispidum</i>	TRSU	0.06	0	0	0.04	0.06	0.06	0.05	0.05
	WCNP	0.14	0.14	0.05	0.29	0.13	0	0.06	0.21
	TRNU	0.1	0.17	0	0.88	0.13	0.06	0.08	0.09
<i>Hordeum jubatum</i>	TRSU	0.2	0.12	0.21	0.86	0.23	0.17	0.16	0.25
	WCNP	0.14	0.14	0.62	0	0.22	0.09	0.29	0.24
	TRNU	0.02	0	0	0.38	0	0	0.02	0.05
<i>Iva axillaris</i>	WCNP	0.01	0	0	0	0	0	0.03	0
	TRSU	0.04	0.06	0	0	0.02	0.13	0.03	0.01
<i>Lepidium densiflorum</i>	WCNP	0	0	0.05	0	0	0	0	0
	TRNU	0.05	0	0.17	0.75	0	0.06	0.08	0.06
	TRSU	0.06	0.06	0.21	0.36	0.04	0.11	0.06	0.11
<i>Oxalis stricta</i>	WCNP	0.05	0	0.19	0	0.03	0	0.06	0.06
	TRNU	0	0	0	0.38	0	0	0	0
	TRSU	0.01	0	0.07	0.39	0	0	0	0.01
<i>Panicum capillare</i>	WCNP	0.01	0	0.57	0.14	0.03	0.09	0.06	0
	TRNU	0	0	0	0	0	0	0.06	0.03
	WCNP	0.05	0	0.05	0	0	0	0	0
<i>Schedonnardus paniculatus</i>	TRNU	0	0	0	0.13	0	0	0	0
	TRSU	0.01	0	0	0.5	0	0	0.02	0
	WCNP	0.01	0.14	0.62	0	0	0	0	0
<i>Sitanion hystrix</i>	WCNP	0.06	0	0	0	0.03	0	0.1	0.09
<i>Verbena bracteata</i>	TRSU	0	0	0	0.18	0	0.02	0	0
	WCNP	0.01	0	0.57	0	0	0	0.06	0
<i>Verbena stricta</i>	WCNP	0.1	0	0.1	0	0	0.27	0.19	0.03
Exotic species									
<i>Agropyron cristatum</i>	TRNU	0.01	0	0	0	0	0.06	0	0
	TRSU	0.02	0	0	0.14	0.08	0.06	0	0
<i>Alyssum desertorum</i>	TRSU	0.01	0	0.07	0.25	0	0.09	0.02	0.04
	WCNP	0	0	0.05	0	0	0	0	0
<i>Bromus inermis</i>	TRNU	0.12	0	0	0	0.27	0.12	0.12	0.09
	TRSU	0.08	0.24	0.36	0	0.17	0.42	0.14	0.07
	WCNP	0.01	0	0	0	0	0	0.03	0
<i>Bromus japonicus</i>	TRNU	0.1	0	0.5	0.63	0.13	0.12	0.12	0.08
	TRSU	0.23	0.29	0.5	0.29	0.21	0.3	0.19	0.24
	WCNP	0.37	0.29	0.48	0.14	0.38	0.09	0.39	0.48
<i>Bromus tectorum</i>	TRNU	0	0	0.17	0.5	0	0	0	0
	TRSU	0	0.06	0.07	0.11	0	0.02	0	0.03
	WCNP	0.07	0	0.29	0	0.06	0	0.1	0.03
<i>Camelina microcarpa</i>	TRSU	0.05	0.12	0.21	0	0.06	0.09	0.08	0.11
<i>Chenopodium album</i>	TRNU	0.02	0	0	0.38	0.07	0.06	0.04	0.08
	TRSU	0.04	0	0.07	0	0.08	0	0.11	0.05
<i>Cirsium arvense</i>	TRNU	0.07	0	0.5	0.75	0.2	0.18	0.08	0.06
	TRSU	0.02	0.06	0.07	0.29	0.02	0	0.03	0.02
	WCNP	0.01	0	0.19	0	0	0	0	0
<i>Convolvulus arvensis</i>	TRNU	0.02	0	0.33	0.5	0	0	0.06	0

Table A1. Continued.

Species	Unit	> 200	PDT 100–200	PDT < 100	PDT within	Road 100–200	Road < 100	Trail 100–200	Trail < 100
<i>Cynoglossum officinale</i>	TRSU	0.01	0.06	0.29	0.46	0.02	0.09	0.02	0.03
	WCNP	0.02	0	0.05	0	0.03	0	0.06	0
	WCNP	0	0	0.05	0	0	0.09	0	0
<i>Descurainia sophia</i>	TRNU	0.01	0	0	0.75	0	0	0.02	0
	TRSU	0.02	0.06	0.14	0.5	0.09	0.08	0.03	0.05
<i>Euphorbia esula</i>	WCNP	0	0	0	0	0.03	0	0	0
	TRSU	0.15	0	0.21	0.04	0.09	0.11	0.27	0.21
<i>Kochia scoparia</i>	TRNU	0.05	0	0	0	0	0	0.04	0.06
<i>Lactuca serriola</i>	TRSU	0	0	0	0.04	0	0	0	0
	TRNU	0.01	0	0	0.25	0	0	0.02	0
	TRSU	0.02	0	0	0.04	0.04	0.02	0	0.02
<i>Lappula echinata</i>	WCNP	0.07	0.14	0.1	0.14	0.13	0	0.19	0.06
	TRSU	0.01	0	0.07	0.14	0	0.02	0	0.01
	WCNP	0	0	0.24	0	0	0	0	0
<i>Lappula redowskii</i>	WCNP	0	0.14	0.14	0	0	0	0.03	0
<i>Marrubium vulgare</i>	WCNP	0	0.14	0.14	0	0	0	0.03	0
<i>Medicago lupulina</i>	TRNU	0	0	0	0.13	0	0	0	0.02
	TRSU	0	0	0	0.04	0	0.05	0	0
	WCNP	0.03	0.14	0.1	0.14	0.06	0	0.16	0
<i>Medicago sativa</i>	TRSU	0	0	0.07	0	0	0	0	0
	WCNP	0.01	0	0	0	0	0	0	0
<i>Melilotus alba</i>	TRNU	0.09	0	0	0	0.07	0.06	0.04	0.06
<i>Melilotus officinalis</i>	TRSU	0.01	0	0	0	0.04	0	0.03	0.01
	TRNU	0.26	0.33	0.5	0.25	0.33	0.71	0.37	0.26
	TRSU	0.4	0.71	0.5	0.89	0.51	0.45	0.48	0.47
<i>Poa compressa</i>	WCNP	0.01	0	0.1	0	0	0	0.06	0.03
	TRNU	0.02	0	0	0	0	0.18	0.04	0.02
	TRSU	0.01	0.06	0	0	0.04	0.02	0	0.04
<i>Poa pratensis</i>	WCNP	0.06	0.14	0.1	0.14	0.16	0.09	0.23	0
	TRNU	0.29	0.17	0.67	0.75	0.67	0.41	0.45	0.24
	TRSU	0.32	0.41	0.5	0.11	0.3	0.48	0.25	0.32
<i>Polygonum aviculare</i>	WCNP	0.68	1	0.38	0.71	0.75	0.91	0.84	0.42
	TRNU	0.01	0	0	0.13	0	0	0	0
	TRSU	0.01	0	0	0.07	0.02	0	0	0
<i>Salsola iberica</i>	WCNP	0	0	0.14	0	0	0	0.03	0
	TRNU	0.04	0	0	0.63	0	0	0	0.03
	TRSU	0.01	0.06	0	0.82	0.04	0.05	0	0.01
<i>Sisymbrium altissimum</i>	TRNU	0	0	0	0.25	0	0	0	0
	TRSU	0	0	0	0.07	0	0	0	0
	WCNP	0	0	0.05	0	0.03	0	0	0
<i>Taraxacum officinale</i>	TRNU	0.21	0.17	0.33	0.38	0.2	0.35	0.18	0.17
	TRSU	0.16	0.06	0.14	0.14	0.26	0.19	0.17	0.15
	WCNP	0.05	0.14	0.43	0.29	0.19	0.09	0.19	0.03
<i>Thlaspi arvense</i>	TRNU	0.01	0	0.17	0.63	0	0	0	0
	TRSU	0	0	0	0.07	0	0	0	0
<i>Tragopogon dubius</i>	WCNP	0	0	0.05	0	0.03	0	0	0
	TRNU	0.18	0.17	0.17	0	0.27	0.29	0.16	0.18
	TRSU	0.21	0.18	0.36	0.04	0.23	0.19	0.2	0.21
<i>Verbascum thapsus</i>	WCNP	0.32	0.57	0.33	0.43	0.56	0.91	0.42	0.39
	WCNP	0.02	0	0.19	0	0.03	0	0	0

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