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ALIEN PLANT INVASION IN MIXED-GRASS PRAIRIE: EFFECTS OF VEGETATION TYPE AND ANTHROPOGENIC DISTURBANCE

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Abstract. The ability of alien plant species to invade a region depends not only on attributes of the plant, but on characteristics of the habitat being invaded. Here, we examine characteristics that may influence the success of alien plant invasion in mixed-grass prairie at Theodore Roosevelt National Park, in western North Dakota, USA. The park consists of two geographically separate units with similar vegetation types and management history, which allowed us to examine the effects of native vegetation type, anthropogenic disturbance, and the separate park units on the invasion of native plant communities by alien plant species common to counties surrounding both park units. If matters of chance related to availability of propagules and transient establishment opportunities determine the success of invasion, park unit and anthropogenic disturbance should better explain the variation in alien plant frequency. If invasibility is more strongly related to biotic or physical characteristics of the native plant communities, models of alien plant occurrence should include vegetation type as an explanatory variable. We examined >1300 transects across all vegetation types in both units of the park. Akaike's Information Criterion (AIC) indicated that the fully parameterized model, including the interaction among vegetation type, disturbance, and park unit, best described the distribution of both total number of alien plants per transect and frequency of alien plants on transects where they occurred. Although all vegetation types were invaded by alien plants, mesic communities had both greater numbers and higher frequencies of alien plants than did drier communities. A strong element of stochasticity, reflected in differences in frequencies of individual species between the two park units, suggests that prediction of risk of invasion will always involve uncertainty. In addition, despite well-documented associations between anthropogenic disturbance and alien plant invasion, five of the six most abundant alien species at Theodore Roosevelt National Park had distributions unrelated to disturbance. We recommend that vegetation type be explicitly taken into account when designing monitoring plans for alien species in natural areas.

Key words: Akaike's Information Criterion; alien plants; anthropogenic disturbance; Great Plains; mixed-grass prairie; native vegetation type; Theodore Roosevelt National Park, North Dakota (USA).

INTRODUCTION

Concern over the invasion of non-indigenous plants into natural areas is rapidly escalating to alarm as the number of studies showing the prevalence and effects of such invasions climbs (Pysek 1995). Case studies have focused on individual plant species and their attributes (Young and Evans 1973, Mack 1981, Vitousek and Walker 1989, Thompson 1991, McClaran and Anable 1992, D'Antonio 1993, Qi and Upadhyaya 1993, Edwards et al. 1995) and several authors have attempted to find trends and generalizations that would help predict plant invasiveness (Andersen 1995, Beerling 1995, Pysek et al. 1995, Rejmanek 1995, 1996, Rejmanek and Richardson 1996, Daehler 1998). The role of anthropogenic and other forms of disturbance in promoting invasions of alien plants is well documented (Belcher and Wilson 1989, Hobbs 1989, Hobbs and Huenneke 1992, D'Antonio 1993, Parker et al. 1993, McIntyre and Lavorel 1994, Greenberg et al. 1997, Stapanian et al. 1998, Smith and Knapp 1999). Stochastic events related to the convergence of appropriate abiotic conditions, propagule availability, and phenological timing have also been implicated in the success or failure of plant invasions (Crawley 1989, Mack 1995), as have characteristics of the invaded vegetation or habitat (Mack 1989, Rejmanek 1989, Knops et al. 1995, Kotanen et al. 1998, Stohlgren et al. 1999).

In this study, we examine the influence of three factors, anthropogenic disturbance, native vegetation type, and park unit (a blocking factor reflecting the two geographically separate park areas) on the species composition of alien plants of Theodore Roosevelt National Park (TRNP) in western North Dakota, USA. The park consists of two units separated by roughly 115 km of federally and privately owned rangeland. The south and

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north units of the park comprise approximately 18 600 and 9600 ha, respectively, of mixed-grass prairie, badlands (an erosional landscape of buttes, tablelands, and valleys), and riparian areas. Twenty-three native vegetation types have been delineated on a geographic information system (GIS; TRNP, *unpublished* [maps available online]),[5] many of which occur in both units. Vegetation types are present in a complex mosaic, with high levels of spatial association among the different plant communities such that propagules in one vegetation type are unlikely to be spatially isolated from most other vegetation types. The configuration of TRNP provided an opportunity to examine the frequency of invasion of a suite of alien species into vegetation types occurring in two natural areas managed in similar ways. In addition, the availability of digitized data for roads, trails, and other human-impacted areas allowed us to examine the effects of anthropogenic disturbance on invasibility of each vegetation type. Because each of the alien species we consider here occurred in counties surrounding both units of the park, and thus had the potential to have colonized both units, we assume that differences in alien plant distribution attributed to park unit are associated with stochastic events (e.g., convergence of appropriate conditions for germination, availability of propagules) that influenced colonization.

The objectives of this research were (1) to compare the effects of vegetation type, anthropogenic disturbance, and park unit on the number and frequency (i.e., number of plots occupied per transect) of alien plant species in native vegetation types common to the north and south units of TRNP and (2) to determine which factors and interactions best explain the presence of individual alien plant species on transects. If matters of chance related to availability of propagules and transient establishment opportunities largely determine the success of invasion, we would predict that park unit or anthropogenic disturbance would better explain the variation in alien plant frequency than would vegetation type. However, if invasibility is more strongly related to biotic or physical characteristics of the native plant communities, we would predict that models of alien plant occurrence would more likely include vegetation type as an explanatory variable.

Methods

Sampling.—To ensure that we sampled all areas of the park, we divided both units of TRNP into rectangular strata, roughly 800 ha each. Using GIS maps, we randomly placed three points in each vegetation type in each stratum and recorded the coordinates so they could be located with Global Positioning System (GPS) units in the field. Transects were oriented perpendicular to elevation contour lines, starting at the edge of the vegetation type and passing through the randomly generated point. The number of plots (0.5 × 2.0 m) on each transect was proportional to the square root of the area of the vegetation type within the stratum; the minimum number of plots on any transect was set at 4, the maximum at 20. Plots were oriented parallel to elevation contour lines and we recorded presence of all species occurring in each plot, although in this analysis we consider only alien species. Analyses involving individual species use number of transects occupied as the response variable, which has the effect of eliminating biases associated with frequency data collected on plots placed systematically (Whysong and Miller 1987), since the sample unit is the transect and these were placed randomly. Occurrences were summed over each transect and divided by the total number of plots on the transect to determine frequency of each plant species on each transect; these values were averaged for all transects on which we found at least one alien species to determine mean frequency of all alien species per transect.

Although it would have been desirable to sample in each unit each year in a random fashion, for logistical reasons the south unit was surveyed in 1996 and the north unit in 1997. Of the alien species we found, yearly changes in population size are likely to be important in *Melilotus officinalis,* which is 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 frequency rather than cover minimizes differences associated with seasonal and yearly fluctuations (Elzinga et al. 1998). Vegetation was sampled between 15 May and 31 September. Taxonomy follows Barker et al. (1986).

We classified transects a posteriori as disturbed if any part fell within 100 m of roads, trails, campgrounds, picnic areas, buildings within the park boundaries, or fields seeded to non-native grasses. Thus, we defined as disturbed that *native* vegetation that occurred within 100 m of any of these features. Campgrounds and picnic areas themselves, for example, are not included in this analysis. Because the perimeter of the park either coincided with a road, which was already considered disturbed, or was adjacent to rangeland, we did not consider the perimeter, per se, disturbed. The 100-m buffers were generated using TNT Mips software (MicroImages, Lincoln, Nebraska, USA).

Although we chose to restrict this analysis to anthropogenic disturbance, we recognize that other forms of disturbance are found in the park, including seasonal flooding in the river bottoms, excavation and grazing in prairie dog towns, and ongoing erosional processes, among others. We also chose not to include an explicit spatial component within park units in our analysis. A preliminary analysis using general linear models revealed no systematic differences in number of alien species or frequency of individual species among strata (*data not shown*); vegetation type accounted for far

[5] ⟨http://www.nps.gov/gis/midwest_data.html#North Dakota⟩

TABLE 1. Properties of vegetation in the north and south units of Theodore Roosevelt National Park, North Dakota, USA.

Vegetation type	North Unit		South Unit		Transects	
	Undisturbed	Disturbed	Undisturbed	Disturbed	Total	Alien (%)
Used in model selection						
Chrysothamnus nauseosus/Agropyron smithii	29	7	55	18	109	53
Artemisia tridentata/Atriplex confertiflora	26	9	51	9	95	59
Populus deltoides/Juniperus scopulorum	18	3	11	1	33	91
Artemisia cana	22	7	45	15	89	94
Symphoricarpos occidentalis/Prunus virginiana	32	4	50	16	102	98
Andropogon scoparius	31	5	56	16	108	68
Andropogon scoparius/Juniperus horizontalis	23	10	57	3	3	63
Stipa comata/Bouteloua gracilis	24	6	32	10	72	75
Juniperus scoparius/Oryzopsis micrantha	26	10	52	11	99	88
Agropyron smithii/Stipa viridula	31	4	58	15	108	95
Agropyron smithii/Stipa comata	32	3	45	15	95	96
Not used in model selection						
Achenbach Hills complex	5	1	0	0	6	83
Populus tremuloides	0	0	3	0	3	100
Symphoricarpos occidentalis	10	5	3	0	18	94
Artemisia tridentata/Bouteloua gracilis	0	0	23	1	24	83
Grassed sand floodplain	19	2	0	0	21	71
Marsh	6	3	0	0	9	67
Petrified Forest complex	0	0	1	2	3	100
Populus tremuloides/Betula occidentalis	4	5	0	0	9	89
River bottom	9	0	17	3	29	100
Rolling scoria complex	0	0	33	12	45	95
Steep scoria complex	0	0	29	10	39	95
Salix spp.	15	3	0	0	18	100

Notes: Alien transects are those with at least one alien plant. "Disturbed" refers to those transects that were within 100 m of a road, trail, seeded field, campground, or picnic area. The vegetation types that were not used in the analysis were excluded because they lacked representation in one of the park units and/or in one disturbance category.

more of the variability in these variables than did stratum.

Data analysis.—Because we were interested in both main effects and interactions, only those vegetation types that included both disturbed and undisturbed transects and that occurred in both the north and south units of the park were used in the analysis, although we describe the excluded vegetation types in general terms as a point of comparison. We used Akaike's Information Criterion (AIC; Burnham and Anderson 1998), which incorporates the log-likelihood with a penalty for added parameters, to determine the best model out of all possible models containing park unit, disturbance, vegetation type, and their interactions. We also used AIC to compare models with only main effects for (1) number of alien species per transect, (2) frequency of alien species on transects that contained at least one alien species (hereafter termed "occupied transects"), and (3) presence/absence of each alien species that occurred on at least 10 transects. The difference between the AIC score for the best model and each model with only one of the explanatory variables is an indication of the relative importance of each variable. We chose to use the information theoretic approach, represented by AIC, rather than a statistical hypothesis testing approach for several reasons. First, our primary goal was to choose the best model out of several potential models, rather than from specific alternatives defined a priori. Second, we were more interested in effect size rather than significance of the various parameters; our sample size was large, so that virtually all factors were *statistically* significant, regardless of their biological significance. Finally, we wanted to compare effect sizes of the three explanatory variables, which we could not do with conventional hypothesis testing procedures, since vegetation type had many more levels and thus accounted for much more of the variation in these kinds of models than did either park unit or disturbance. All analyses were done using Proc Mixed (SAS Institute 1992).

RESULTS

Of 847 transects in the south unit, only 110 (13%) were free of alien plants; in the north unit, 121 (26%) of the 467 transects were free of alien plants. We found 38 alien plant species on our transects (Appendix), of which 27 occurred in both units and 11 species occurred only in the south unit. Seventeen alien species occurred on at least 10 transects and thus were analyzed individually. Eleven of the 23 vegetation types occurred in both the north and south units and had both disturbed and undisturbed transects (Table 1). Of the 17 species analyzed individually, eight occurred at least once in each of the 11 vegetation types in our analysis; 15

TABLE 2. Variables included in the three best models of vegetation structure, as determined by Akaike's Information Criterion (AIC).

Response variable	Sample size (no. transects)	Best model (difference in AIC score from second)	Second-best model (difference in AIC score from third)	Third-best model (difference in AIC score from fourth)	Difference in AIC score from best for each main effect		
					V	U	D
Total number of alien species	1003	V × U × D (32)	V × U (18)	V, U, D (4)	69	258	265
Mean frequency of alien species	796	V × U × D (74)	V × D (1)	V × U (30)	108	217	219
Salsola iberica	27	V (3)	V, D (1)	V, U (3)	0	44	43
Tragopogon dubius	242	V (2)	V, U (1)	V, D (1)	0	83	83
Bromus japonicus	204	V, U (1)	V × U (1)	V, U, D (10)	12	108	121
Melilotus officinalis	434	V, U or V, U, D (5)	V × U (1)	V or V, D or V × U × D (1)	6	22	27
Taraxacum officinale	225	V, U or V × U (3)	V or V, U, D (2)	V, D (5)	3	74	78
Camelina microcarpa	68	V × U (14)	V × U × D (5)	V, U or V, U, D (14)	33	85	98
Cirsium arvense	39	V × U (15)	V × U × D (15)	V, U (2)	32	72	80
Euphorbia esula	112	V × U (18)	V × U × D (37)	V, U (2)	98	112	148
Poa pratensis	377	V × U (7)	V (1)	V, U (1)	7	172	172
Descurainia sophia	37	D, U or D × U (1)	D (1)	U (8)	13	2	1
Convolvulus arvensis	34	D (2)	D × U (1)	U (1)	4	3	0
Poa compressa	25	U (1)	D (3)	U, D (1)	10	0	1
Lactuca serriola	17	U (2)	D (1)	U, D (3)	26	0	2
Chenopodium album	59	D (1)	U (3)	U, D (1)	14	1	0
Alyssum desertorum	13	D or U, D (1)	U or D × U (21)	V, U, D (2)	24	1	0
Agropyron cristatum	25	U or D (2)	U, D (2)	U × D (7)	11	0	0
Bromus inermis	144	V, D or V × D (1)	V, U, D (7)	V (1)	8	46	38

Notes: Numbers in parentheses report the difference between the AIC score for that model and for the next-best model. The final three columns indicate the difference in AIC score between models containing each main effect alone and the best model. The magnitude of the AIC score is dependent on sample size, so scores can only be compared among models for a given response variable. The difference in AIC scores between models reflects uncertainty in model selection, with relatively small differences indicating greater uncertainty. V = native vegetation type, U = park unit, D = anthropogenic disturbance. Variables separated by "×" or commas indicate interaction between main effects or main effect without interaction, respectively.

occurred in seven or more vegetation types. Thus, propagules generally were not isolated from any of the vegetation types in the analysis. Seventy-six and 77% of transects in the north and south units, respectively, were located in the 11 vegetation types. In the south unit, 23% of all transects and 20% of those in the 11 selected vegetation types were classified as disturbed; in the north unit, 21% of all transects and 19% of those in the selected vegetation types were classified as disturbed. The number and frequency of alien species were higher in vegetation types excluded from the analysis (2.7 ± 0.13 vs. 2.1 ± 0.06 alien species/transect and 34.6 ± 1.4 vs. 27.8 ± 0.66% of plots occupied/transect in excluded and included vegetation types, respectively).

Number and frequency of alien species.—The number and frequency of alien plant species depended on the interaction among all three variables: vegetation type, disturbance, and park unit (Table 2). In each case, vegetation type as a main effect had the least difference in AIC score from the best model (Table 2), which indicated that this variable had the largest effect on the number and frequency of alien plants.

The number of species per transect varied more among than within vegetation types (Fig. 1a). For the most part, the interactions reflected the magnitude rather than direction of differences in numbers of alien species. The number of alien species on disturbed transects either did not differ from, or was greater than, the number on undisturbed transects, regardless of vegetation type or park unit. However, in *Agropyron smithii/Stipa viridula* and *Populus deltoides/Juniperus scopulorum* vegetation types, disturbed transects in the north unit had far more alien species than did undisturbed transects. This was true for *A. smithii/S. viridula* but not for *P. deltoides/J. scopulorum* vegetation in the south unit, where both disturbed and undisturbed transects had very high numbers of alien species. With a single exception (in *A. smithii/S. viridula* vegetation), the number of alien species per transect in the south unit was the same as or greater than the number in the north unit in each vegetation type.

There was less variation in frequency of alien species on occupied transects than there was in number of alien species (Fig. 1b). Frequency was, in fact, only very weakly related to number of species ($r = 0.07$, $P = 0.046$). Differences between frequencies of alien plants on disturbed and undisturbed transects in general were small, as were differences between the north and south units. Interaction among the three variables was primarily evident in *Juniperus scopulorum/Oryzopsis micrantha*, where disturbed transects had higher frequencies of aliens in both north and south units, and in *Symphoricarpos occidentalis/Prunus virginiana* vege-

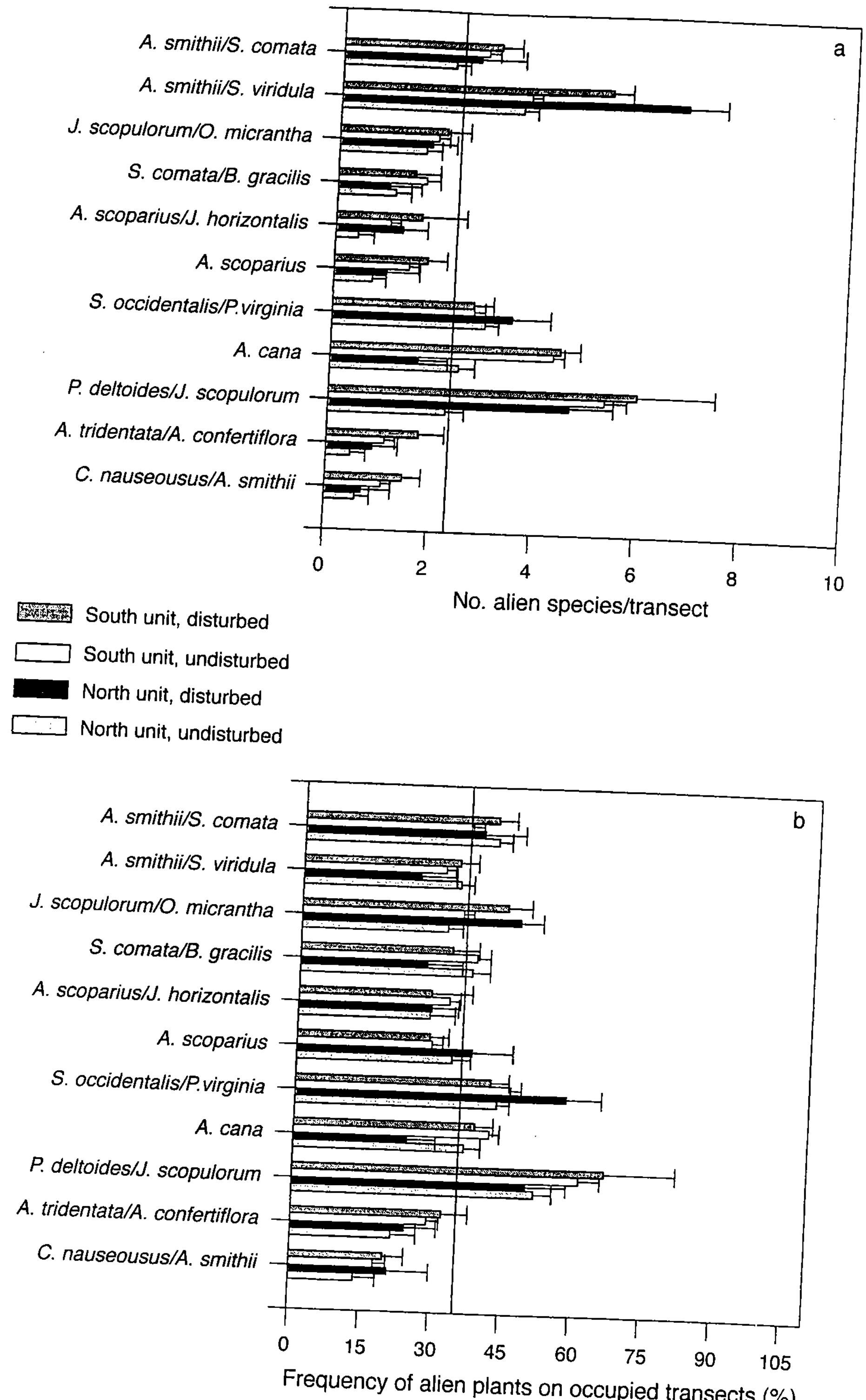

FIG. 1. Akaike's Information Criterion identified the fully parameterized model, including the vegetation type × park unit × disturbance interaction, as the best model for both (a) mean number of alien species on transects and (b) mean frequency of alien plants on occupied transects. Shown are least-squares means with 1 SE. The vertical line on each graph represents the mean of the least-squares means, as a point of reference.

tation, where disturbed transects had higher frequencies only in the north unit. Again, it was the magnitude rather than the direction of differences in frequency that resulted in the interaction: alien species were never more frequent on undisturbed compared with disturbed transects and in only one vegetation type were they more frequent in the north than in the south unit.

Presence of individual alien species on transects.— AIC identified, either as a main effect or as an interaction, vegetation type as a variable in the best model for 10 species, park unit for 12 species, and disturbance for seven species (Table 2). For the seven species best described by either park unit or disturbance, AIC scores differed little between models containing either variable. This suggests considerable uncertainty in model selection between these two variables. In general, vegetation type was unlikely to be included in models for those species that occurred infrequently. Vegetation type more closely approximated the best model (and therefore had the largest effect in the model) for seven species, park unit and disturbance for six; the remainder were either well defined by interactions present in the best model (e.g., *Cirsium arvense, Camelina microcarpa,* and *Euphorbia esula*), or showed little difference among any of the models (e.g., *Convolvulus arvensis)* (Table 2).

For two species, *Tragopogon dubius* and *Salsola iberica,* the best model included only vegetation type (Table 2). *Tragopogon dubius* was most likely to occur in grasslands dominated by cool-season grasses with little or no shrub or tree canopy (Fig. 2a). *Salsola iberica* occurred most often on transects in the *Chrysothamnus nauseosus/Agropyron smithii* vegetation type, which is primarily composed of bare ground, and was never recorded in vegetation types dominated by sod-forming grasses (Fig. 2a).

The best models for *Bromus japonicus* and *Melilotus officinalis* included vegetation type and park unit as main effects (Table 2). In each case, vegetation type had a larger effect than park unit as indicated by the smaller difference in AIC score between the main effect of vegetation type and the best model. Both species tended to be more commonly encountered in the south unit, but relative occurrence among vegetation types was similar in both units (Fig. 3a, b). The best models for *Camelina microcarpa. Cirsium arvense, Euphorbia esula,* and *Poa pratensis* included the interaction between vegetation type and park unit (Table 2). The AIC score was the same with and without this interaction term for *Taraxacum officinale,* and vegetation type alone had nearly as high a score as the two-term model (Table 2). *Taraxacum officinale* occurred on either the same or greater proportion of transects in the north than in the south unit in each vegetation type (Fig. 3c). *Camelina microcarpa. Cirsium arvense,* and *Euphorbia esula* frequencies were strongly defined by the interaction; main effects alone had relatively large differences in AIC scores from the best model. *Camelina microcarpa* was very uncommon in the north unit, but occurred there in the two vegetation types in which it was most common in the south unit (Fig. 3d). *Cirsium arvense* was unusual in that it was more commonly encountered in the north than the south unit, and occurred in the south unit in vegetation types different from where it occurred in the north (Fig. 3e). *Euphorbia esula* varied substantially among vegetation types in the south unit, and although present on two transects in the north unit, was absent from the 11 vegetation types in this analysis (Fig. 3f). *Poa pratensis* was more frequently encountered in the south unit than the north in *Populus deltoides/Juniperus scopulorum* vegetation. but was more common in the north unit in *Agropyron smithii/Stipa viridula* and *Symphoricarpos occidentalis/Prunus virginiana* vegetation (Fig. 3g).

The best models for *Lactuca serriola, Poa compressa, Agropyron cristatum, Alyssum desertorum, Chenopodium album,* and *Convolvulus arvensis* included either park unit or disturbance as main effects, although AIC did not distinguish well between the two variables (Table 2). All of these species occurred relatively infrequently in the vegetation types under consideration. *Agropyron cristatum* and *L. serriola* tended to be more common in the south unit, *P. compressa* in the north unit (Fig. 4). Where significantly different. each species was more commonly encountered on disturbed than on undisturbed transects (Fig. 4). *Descurainia sophia* was the only species for which the interaction between disturbance and park unit defined the best model (Table 2). This species was far more common on disturbed than undisturbed transects in the south unit, but did not differ by disturbance in the north unit, where it was substantially less abundant (Fig. 4). The best model for *Bromus inermis* included the interaction between vegetation type and disturbance. the only species for which this was the case (Table 2). However, the model containing all three main effects (but no interaction) differed from the best model by only one unit (Table 2). *Bromus inermis* was always more commonly encountered on disturbed transects. especially in the *Agropyron/Stipa* communities (Fig. 5).

Discussion

Our results indicate that biotic and/or physical characteristics of the site are highly important in determining overall invasibility in this mixed-grass prairie system. Vegetation type had a larger effect (i.e., an AIC score that differed less from the best model) than either park unit or disturbance when alien species were considered in aggregate and for ten of the 17 species considered individually (Table 2). Nonetheless, the presence of interactions means that for most species (Figs. 3 and 5), and for alien species considered in aggregate (Fig. 1), the effect of park unit and disturbance also must be considered when interpreting alien species distributions among vegetation types.

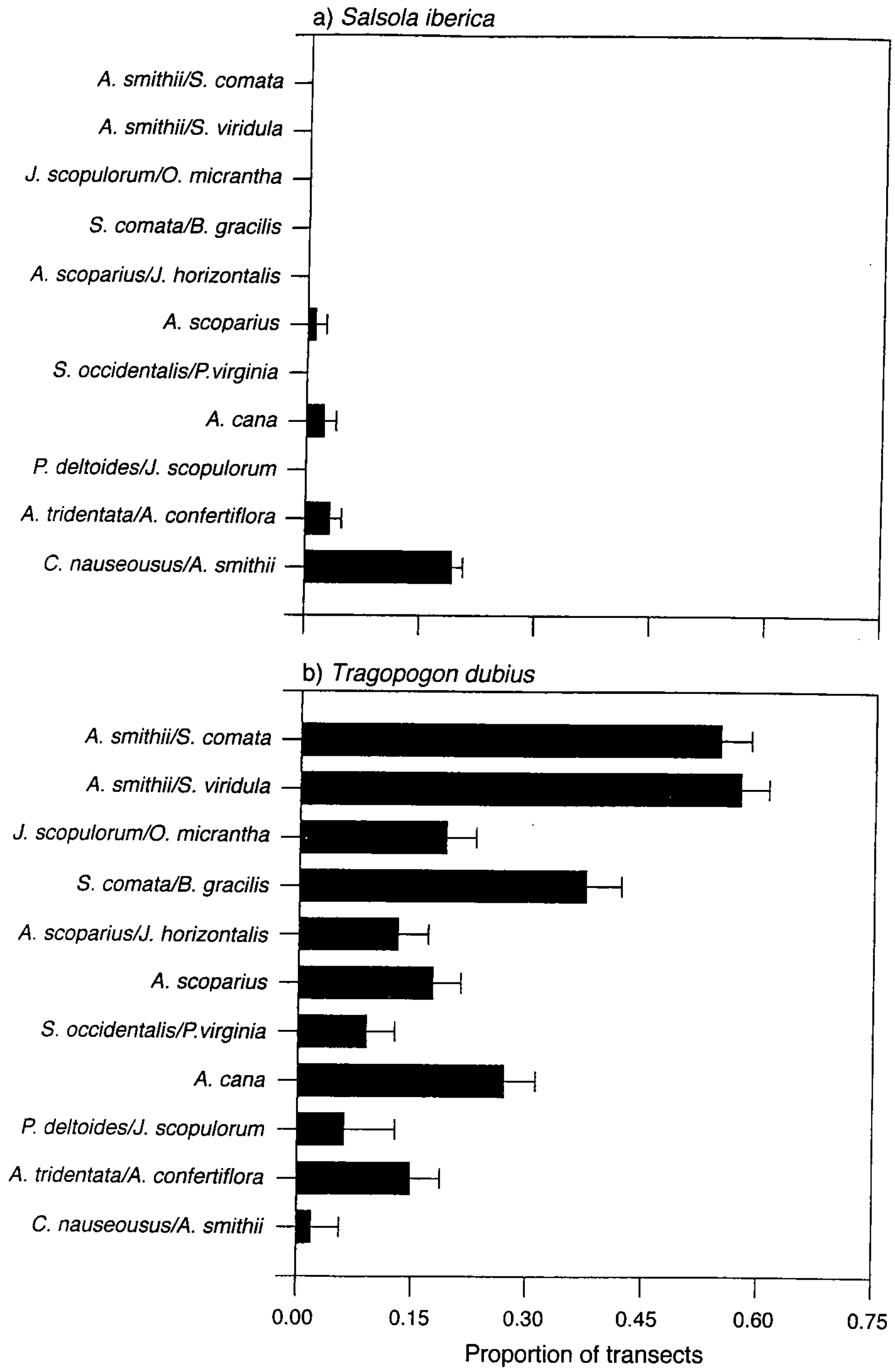

FIG. 2. Proportion of transects on which *Salsola iberica* and *Tragopogon dubius* were found in 11 vegetation types at TRNP. Shown are least-squares means with 1 SE.

The presence of a three-way interaction in the best model for number and frequency of alien species in aggregate, which did not occur for any individual species (Table 2), suggests that the interaction is an emergent property of the alien species assemblage, which combines soil and water tolerances and the establishment requirements of each individual species. Mixed-grass prairie in this region is thought, based largely on observations in shortgrass and tallgrass prairies (Daubenmire 1978, Burke et al. 1997), to be limited by nitrogen and water; our explanatory variables likely reflect differences in these resources. Roads and trails are often characterized as conduits for the transport and/or dispersal of alien plants (Tyser and Worley

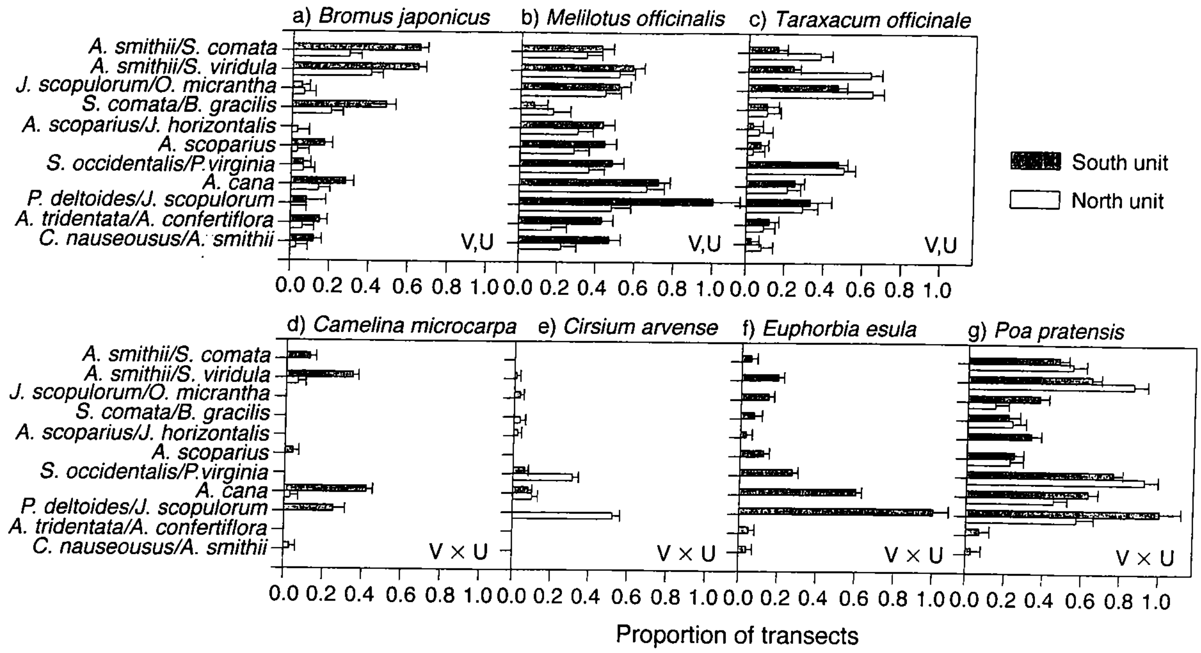

FIG. 3. Proportion of transects on which alien species were found in 11 vegetation types, by park unit. Vegetation type and park unit were main effects in models for *Bromus japonicus, Melilotus officinalis,* and *Taraxacum officinale;* for *Camelina microcarpa, Cirsium arvense, Euphorbia esula,* and *Poa pratensis,* models also included the interaction between vegetation type and park unit. Shown are least-squares means with 1 SE.

1992, Knops et al. 1995, Kotanen et al. 1998). Some have suggested that soil moisture is enhanced by runoff from paved roadways (McIntyre and Lavorel 1994, Kotanen et al. 1998). Vegetation types themselves vary in available water and nutrients. *Andropogon scoparius* is a very efficient competitor for nitrogen (Wedin and Tilman 1993), which may limit the nutrient's availability to aliens and thus compromise their ability to invade vegetation types dominated by this species (Fig. 1). Vegetation types that occur near rivers, tributaries, and drainages and on north-facing slopes are more mesic than those on uplands and south-facing slopes (Hanson and Whitman 1938, Whitman and Wali 1975). Although mesic vegetation types at TRNP tended to have greater richness and/or frequency of alien plants (e.g., *Symphoricarpos occidentalis/Prunus virginiana, Artemisia cana,* and *Populus deltoides/Juniperus scopulorum* had relatively more alien species at higher frequency than drier *Stipa comata/Bouteloua gracilis, Artemisia tridentata/Atriplex confertiflora,* and *Chrysothamnus nauseosus/Agropyron smithii*), disturbance seemed to favor aliens in only four vegetation types (*Agropyron smithii/Stipa viridula* [number] and *Juniperus scopulorum/Oryzopsis micrantha* [frequency] in both units, *S. occidentalis/P. virginiana* [frequency] and *P. deltoides/J. scopulorum* [number] in the north unit). Compared with *A. smithii/S. comata* vegetation, in which disturbance did not influence invasibility, water availability is greater in *A. smithii/S. viridula* (Hanson and Whitman 1938, Redmann 1975). Added moisture along roadways may have allowed those alien species that were more water-limited to establish, and from there disperse into vegetation types where water was relatively more available. The difference between north and south units may reflect the presence of *Euphorbia esula* in mesic areas of the south unit (Fig. 3f). This highly invasive weed displaces native vegetation (Belcher and Wilson 1989), and also may outcompete many alien species.

Those species that occurred infrequently (with the exception of *Salsola iberica*) were unlikely to vary significantly with vegetation type (Table 2). There are three potential reasons for this observation. One explanation is simply a matter of sample size: because there were 11 vegetation types, only uncommon species that were concentrated in a small number of these types, such as *S. iberica* was, could possibly show a detectable effect. Infrequent clonal species, which are typically undersampled by frequency techniques, were likely missed entirely (e.g., *Hyoscyamus niger* appeared on only one transect, *Sonchus arvensis* on only four [Appendix]). Two other explanations are more biologically interesting, but these require further investigation. First, it is likely that stochastic events and disturbance are more important early in an invasion (Mack 1995). As a species becomes more abundant, differences in survival among vegetation types will become evident. This scenario predicts that species we found infrequently will either increase or decrease over time. The second of these explanations is that the species that occurred infrequently are limited by the availability of disturbed sites, and/or are at the mercy of stochastic

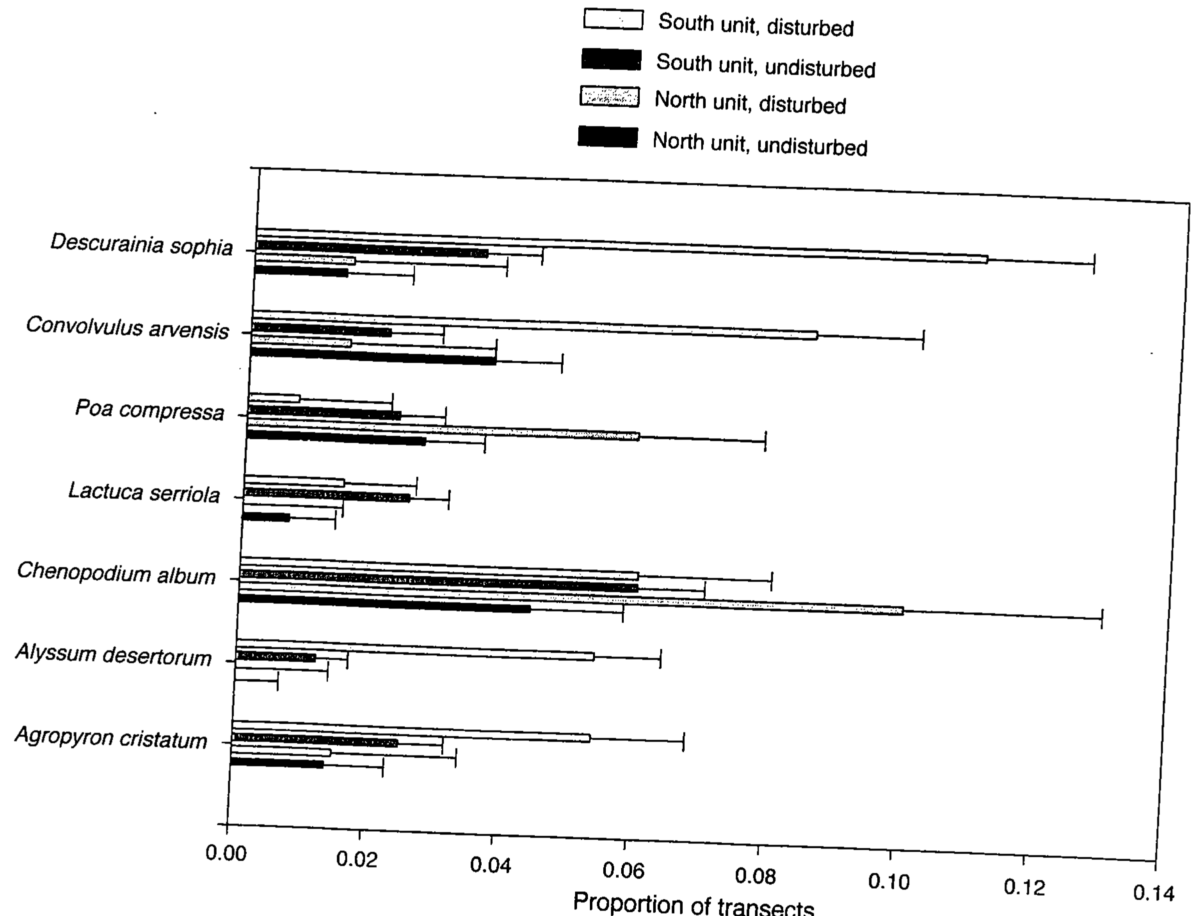

FIG. 4. Proportion of transects occupied by species for which the best model contained park unit and/or disturbance. AIC did not differentiate these two variables well, so both effects are depicted. Shown are least-squares means with 1 SE.

events to arrive at these sites at appropriate times. This scenario predicts that these species always will be encountered at low frequencies and independent of biotic interactions. Control of such species, which are unlikely to pose a threat to undisturbed native communities, would be a lower priority than control of species whose populations are likely to change unpredictably (Hiebert 1997).

Our results are consistent with a large body of research that has demonstrated greater invasion into riparian zones and mesic sites (Rejmanek 1989, DeFerrari and Naiman 1994, Planty-Tabacchi et al. 1996, Kotanen et al. 1998, Stohlgren et al. 1998). Riparian vegetation types (*P. deltoides/J. scopulorum* and *A. cana*) and hardwood draws (*S. occidentalis/P. virginiana*) were among the most heavily infested at TRNP, both in terms of the number of alien species and their frequency on transects (Fig. 1). The high frequency of alien plants in these vegetation types is noteworthy in that it may suggest greater impact to these native communities than, for example, to *A. smithii/S. viridula*, which also has large numbers of alien species (Fig. 1a) but at a frequency near the average for all vegetation types (Fig. 1b). Two xeric vegetation types, *Chrysothamnus nauseosus/Agropyron smithii*, which is dominated by bare ground, and *Artemisia tridentata/Atriplex confertiflora*, had both low numbers of alien species and low frequencies on infested transects (Fig. 1). As Rejmanek (1989) pointed out, however, using survey data it is not possible to separate resistance of the biotic community to invasion from resistance of the abiotic environment, so reasons for the differences in alien richness and frequency among vegetation types cannot be determined from the current study.

Care must be taken in the interpretation of frequency data with respect to ecosystem effects. Although frequency is not necessarily correlated with cover or biomass, it seems intuitively reasonable that the more often a species is encountered in a defined area, the more likely it is that the species may exert an influence on that plant community. However, the shape of the sampled area and the location of sample units are important in interpreting frequency data (Whysong and Miller 1987, Bonham 1989). Our sample units, transects, were long and arrow and likely undersampled clonal invasives with patchy distributions such as *Bromus inermis*

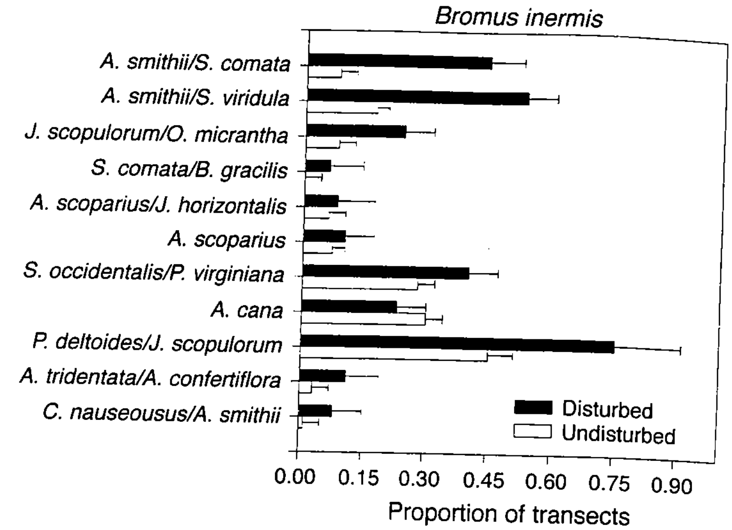

FIG. 5. Proportion of transects occupied by *Bromus inermis*, for which the best model contained the interaction between vegetation type and disturbance. Shown are least-squares means with 1 SE.

and *Cirsium arvense*. We thus may underestimate the effects of such species. Likewise, frequency data typically overestimate species that may be sparsely but evenly distributed (Elzinga 1998). *Bromus japonicus* and *Tragopogon dubius* may fit into this category. We have minimized these effects by using the randomly located transect, rather than plots on transects, as our sample unit for number of alien species and for individual alien species: a species was either present or absent in these analyses. Where we did use frequency of occurrence on transects, we averaged over all species, which minimized the effect of any one growth form.

Transects excluded from this analysis (Table 1) support the notion that mesic and riparian areas are more invasible than drier vegetation types at TRNP. Alien species were found on all transects in river bottom and *Salix* vegetation types. Grassed sand floodplain, which is scoured by ice most years, supports fewer alien plants, perhaps because of the especially harsh conditions. *Populus tremuloides/Betula occidentalis*, another heavily infested community, occurs at the higher elevations of hardwood draws in the north unit, just above the *Symphoricarpos occidentalis/Prunus virginiana* vegetation type. Many of the excluded vegetation types (e.g., marsh, *S. occidentalis*, and *Populus tremuloides*) occur in small patches, which have been shown to be more invasible in other regions (Kemper et al. 1999, Harrison 1999*a*). Vegetation complexes, which are a fine-grained mosaic of variously dominant species, are more heavily invaded than might be anticipated based on soil and moisture properties. Scoria is clay that has been baked by burning lignite, for example, and would not be considered mesic, yet is highly invaded (Table 1). Stohlgren et al. (1999) suggested that species-rich grasslands may be more easily invaded, in part, because "transient" species (those that occur infrequently) result in incomplete utilization of nutrients at local scales. Such a mechanism may explain the unexpectedly high levels of alien infestation in vegetation complexes at TRNP.

Several authors have asserted that all habitats or communities are invasible (e.g., Crawley 1987, Usher 1988, Williamson 1996). Our data support this assertion; none of the vegetation types we surveyed were free of alien plants (Fig. 1). Williamson (1996: 56) further stated, ". . . all communities are more or less equally invasible". This seems not to be the case in many systems (e.g., Rejmanek 1989, Harrison 1999*b*, Stohlgren et al. 1999), including mixed-grass prairie at TRNP. Whether one considers susceptibility to invasion of a single species (e.g., Figs. 2 and 3), or to alien species as a group (Fig. 1), substantial variation existed among vegetation types at TRNP. At a larger scale, Stohlgren et al. (1999) found differences in alien plant invasion among various grassland types, ranging from shortgrass to tallgrass prairie, which they related to differences in native species richness, fertility, and grazing history. Harrison (1999*a*, *b*), working in serpentine and nonserpentine meadows in California, likewise found differences in alien invasion that she attributed to soil nutrient characteristics. Rejmanek (1989) found evidence for greater invasion in mesic and early successional communities. Our results are consistent with the idea that both water and nitrogen limitation may influence the number of alien plants in different vegetation types at TRNP. Appropriate experiments would be necessary to determine cause and effect, however.

In general, the interaction between vegetation type and park unit reflected shifts between which unit had the highest proportion of a taxon in a given vegetation type, rather than major differences in vegetation types occupied in the north and south units. For example, *Poa pratensis* was more commonly encountered in the south unit in *P. deltoides/J. scopulorum* and in the north unit in *Agropyron smithii/Stipa viridula*; nonetheless, the species was relatively common in both vegetation types in both park units (Fig. 3g). Exceptions to this pattern were *Cirsium arvense* and *Camelina microcarpa*, which occurred at vastly different frequencies between units (Fig. 3d, e), and *Euphorbia esula* (Fig. 3f), which in the north unit is confined to the river bottom. *Bromus japonicus* and *Melilotus officinalis* were always more commonly encountered in the south unit than in the north, when they differed, but relative frequency among vegetation types was similar between units (Fig. 3a, b). Because these two species are an annual and a biennial, respectively, and the extensive *M. officinalis* seedbanks are known to respond dramatically to favorable germination conditions (Turkington et al. 1978), the difference in frequency between the two park units may reflect differences in temperature and precipitation between the two years in which the units were surveyed, rather than conditions specific to the units.

The frequency with which park unit and disturbance were indistinguishable in their effect on species distributions (Table 2) suggests similar underlying processes. A likely commonality is stochastic events that influence propagule availability and conditions for seedling establishment. Stochasticity may act at multiple scales. Disturbance, as we defined it, reflects stochastic events at a local scale, park unit at a regional scale. Mack (1995) emphasized the importance of environmental stochasticity in the early establishment of immigrant species. At TRNP, if park unit does reflect stochastic events, the effect persisted in several alien species that were abundant and seemingly well past the establishment phase (Table 2, Fig. 2). Models for these species also included vegetation type, either as a main effect or interaction with park unit, and park unit as a main effect usually had an AIC score closer to the best model than did disturbance (Table 2). This suggests the possibility of systematic differences between the two park units that maintain plant populations at different levels. Disturbance, on the other hand, mainly influenced distributions of less common species (Table 2, Fig. 4), although *Bromus inermis* (Fig. 5) was an exception. For these infrequent species, AIC scores for disturbance and park unit differed by no more than one or two points from each other. The ambiguity in these models may reflect inadequate sampling of uncommon species, although a clear distinction was made between vegetation type and the other two main effects.

Communities of large herbivores may account for some of the observed differences between the north and south units. Although bison (*Bison bison*) stocking rates are similar in the two units, both elk (*Cervus elaphus*) and feral horses occur only in the south unit. In the absence of most predators, herds of all three species require periodic thinning to protect park habitat. Grazing by native ungulates and feral horses likely decreases the dominance of some native species; in tallgrass prairie decreased dominance has been related to increased invasibility (Smith and Knapp 1999), although the reverse has been shown in shortgrass steppe (Milchunas et al. 1992).

Because we have restricted our analysis of disturbance to only those attributed to human endeavor, we have not accounted for all disturbances that occur in the park. In fact, disturbance as we have defined it may be qualitatively different from natural disturbances (see Hobbs and Huenneke 1992). For example, there are several large prairie dog (*Cynomys ludovicianus*) towns in both park units and bison activity results in disruption of native sod at both large and small scales in both units. The overall effect of many natural disturbances at TRNP is to produce changes in continuity of the vegetative canopy and thus increase the number of safe sites for seedling establishment. On the other hand, disturbance associated with roads, campgrounds, and the like, more often takes the form of increased density of alien propagules through seeding for stabilization and landscaping and inadvertent introduction of propagules by humans and livestock. In particular, those areas seeded to dense, sod-forming aliens, such as *Bromus inermis*, probably have fewer opportunities for seedling establishment than many of the native vegetation types. One exception to these differences between natural and anthropogenic disturbance is the Little Missouri River. Riparian areas have been described as dispersal corridors for alien species (DeFerrari and Naiman 1994). In this case, the natural disturbance is not only a source of propagules, but also provides establishment sites through seasonal flooding and ice scouring. This, along with greater access to moisture near the soil surface, likely provides an environment favorable to establishment of many alien species at TRNP.

The effect of anthropogenic disturbance at TRNP was invariant, in that no alien species was significantly more common on undisturbed transects (Figs. 4 and 5). Of those species associated with disturbed transects, two were grasses widely planted either for roadside stabilization or for forage (*Agropyron cristatum* and *Bromus inermis*). Thus, their introduction into TRNP was actively promoted through cultivation and the propagule bank was undoubtedly enhanced through this process. Tyser and Worley (1992) similarly found that disturbance, in the form of road corridors, influenced the number of alien species that invaded adjacent native grasslands. They suggested that not only were roadside plantings responsible for high numbers of aliens adjacent to roads, but that livestock contributed to the further dispersal of alien plants along trails and into the back country. Horseback riding is permitted at TRNP and concessioners' horses have been allowed to roam the south unit, perhaps contributing to the broad distribution of palatable alien grasses throughout the park.

Two other species that were more common on disturbed transects in at least one park unit, *Convolvulus* *arvensis* and *Chenopodium album*, are widely distributed agricultural weeds that are often introduced as contaminants of seed. Because anthropogenic disturbance at TRNP includes areas that have been seeded during construction, these species also may have been planted, albeit inadvertently. Nonetheless, their spread into native vegetation types is associated with proximity to disturbance.

An important outcome of our research is the demonstration that different alien species respond differently to both disturbance and native vegetation type. As Stohlgren et al. (1999) pointed out, sweeping generalizations about alien species are not justified if individual species do not respond in concert to disturbance. We would add that native plant communities vary in their susceptibility to invasion: variation in distributions of the most frequently encountered alien species at TRNP was related to native vegetation type, not disturbance (cf. *Tragopogon dubius*, *Euphorbia esula*, *Poa pratensis*, *Bromus japonicus*, and *Melilotus officinalis*, Figs. 2 and 3).

Management Implications

Planting alien species, for whatever reason, within or near the boundaries of a natural area is risky. *Bromus inermis* is clearly a threat to native vegetation in the vicinity of the roads where it was planted. The extent to which it might spread over time is yet unknown. Weedy contaminants of seed may also be dispersed into native vegetation. The additional cost of obtaining native seed is likely small compared to the cost of eradicating an unwanted alien invader.

Vegetation type matters. Some are more at risk to invasion by alien species than others, and thus will require more intensive management if alien species are to be excluded. As in other studies (DeFerrari and Naiman 1994, Planty-Tabacchi et al. 1996, Stromberg et al. 1997, Stohlgren et al. 1998), riparian areas seem especially at risk. Disturbance, as we defined it in this study, was rarely associated with the most abundant alien species (e.g., *E. esula*, *M. officinalis*, and *P. pratensis*), which suggests that simply limiting construction of roads, trails, and other facilities will not protect vulnerable areas from invasion.

Differences in the frequencies of alien species between the two park units at TRNP suggest that prediction will always be uncertain. A monitoring plan that emphasizes the most vulnerable vegetation types and includes searches for all known potential invaders is critical for early detection as well as to determine which species are, in fact, increasing in number and range. Such strategic planning is an important first step in prioritizing use of limited resources for alien plant control.

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APPENDIX

A table listing the numbers of transects on which we found alien species in the north and south units (467, and 847 were sampled) of Theodore Roosevelt National Park, North Dakota, USA is available in ESA's Electronic Data Archive: *Ecological Archives* A011-003.