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Riparian zones as havens for exotic plant species in the central grasslands

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Abstract

In the Central Grasslands of the United States, we hypothesized that riparian zones high in soil fertility would contain more exotic plant species than upland areas of low soil fertility. Our alternate hypothesis was that riparian zones high in native plant species richness and cover would monopolize available resources and resist invasion by exotic species. We gathered nested-scale vegetation data from 40 1 m^2subplots (nested in four 1000 m^2 plots) in both riparian and upland sites at four study areas in Colorado, Wyoming, and South Dakota (a total of 320 1 m^2subplots and 32 1000 m^2 plots). At the 1 m^2 scale, mean foliar cover of native species was significantly greater ($P < 0.001$) in riparian zones (36.3% ± 1.7%) compared to upland sites (28.7% ± 1.5%), but at this small scale there were no consistent patterns of native and exotic species richness among the four management areas. Mean exotic species cover was slightly higher in upland sites compared to riparian sites (9.0% ± 3.8% versus 8.2% ± 3.0% cover). However, mean exotic species richness and cover were greater in the riparian zones than upland sites in three of four management areas. At the 1000 m^2 scale, mean exotic species richness was also significantly greater ($P < 0.05$) in riparian zones (7.8 ± 1.0 species) compared to upland sites (4.8 ± 1.0 species) despite the heavy invasion of one upland site. For all 32 plots combined, 21% of the variance in exotic species richness was explained by positive relationships with soil % silt ($t = 1.7$, $P = 0.09$) and total foliar cover ($t = 2.4$, $P = 0.02$). Likewise, 26% of the variance in exotic species cover ($\log_{10}$ cover) was explained by positive relationships with soil % silt ($t = 2.3$, $P = 0.03$) and total plant species richness ($t = 2.5$, $P = 0.02$). At landscape scales (four 1000 m^2 plots per type combined), total foliar cover was significantly and positively correlated with exotic species richness ($r = 0.73$, $P < 0.05$) and cover ($r = 0.74$, $P < 0.05$). Exotic species cover ($\log_{10}$ cover) was positively correlated with $\log_{10}$% N in the soil ($r = 0.61$, $P = 0.11$) at landscape scales. On average, we found that 85% (±5%) of the total number of exotic species in the sampling plots of a given management area could be found in riparian zones, while only 50% (±8%) were found in upland plots. We conclude that: (1) species-rich and productive riparian zones are particularly invasible in grassland ecosystems; and (2) riparian zones may act as havens, corridors, and sources of exotic plant invasions for upland sites and pose a significant challenge to land managers and conservation biologists.

Introduction

There is a long standing paradigm by Darwin (1859), Elton (1958), Tilman (1997), and others that exotic species might more easily invade areas of low species diversity than areas of high species diversity. It is commonly thought that the native plants in areas of high species diversity should use limiting resources more completely, preventing invasion by a potentially competing species (MacArthur & Wilson 1967; Tilman 1982, 1997; Fox & Fox 1986; Pimm 1991; McNaughton 1983). Several mathematical models also suggest that areas of high species diversity should be resistant to invasion (Turelli 1981; Post & Pimm 1983; Rummel & Roughgarden 1983; Case 1990).

However, a recent study in the west-central United States showed that rangelands and mountain meadows high in plant species richness, foliar cover, and soil fertility contained more exotic plant species than areas of low plant species richness (Stohlgren et al. 1998a). That study supported an alternate theory that highly diverse plant communities are intrinsically unstable with some species dropping in and out routinely (May 1973). Some native species dropping out might be replaced by exotic species. Huston and DeAngelis (1994) demonstrate theoretically that a large number of species can coexist as a result of biogenic small-scale heterogeneity and interactions among organisms for spatially and temporally variable resources. Under this scenario, exotic plant species might invade and coexist with high numbers of native plant species as long as resources such as light, water, and nutrients were not limiting. Proximity to infested areas might also be important (Stohlgren et al. 1998a). Of particular concern to land managers and conservation biologists is whether riparian zones may be easily invaded despite high soil fertility and high native species richness and cover, and whether riparian zones may act as havens (and sources) of exotic plant invasions.

Some field observations support the notion that species-rich riparian zones in some areas in the northwestern U.S. are more prone to invasion than upland forests that are species-poor (DeFerrari & Naiman 1994) due to intermittent disturbances (flooding) and higher light conditions. Ferreira and Moreira (1995) found a higher degree of invasion in riverine habitats in Central Portugal, due primarily to agricultural disturbance. These observations raise the possibility that species-rich communities that receive some level of disturbance (e.g., fire, herbivory, flooding) may have more resources available, at least temporarily, for invading species (Robinson et al. 1995). However, we found no two studies that used consistent sampling of vegetation and soils in upland and riparian zones in different management areas, so it was difficult to synthesize information about riparian zones and plant diversity. Recognizing these problems, we designed a study that used standardized multi-scale sampling techniques (Stohlgren et al. 1995, 1998a) with adequate replication in upland and riparian zones in four management areas in three states.

Our study objectives were to: (1) assess patterns of exotic plant invasions in riparian and upland sites using a standardized, multi-scale vegetation sampling technique; and (2) evaluate the relationship of native and exotic species richness and foliar cover at multiple spatial scales (e.g., subplot-, plot-, and vegetation type-scales) relative to soil characteristics (texture, %N, %C).

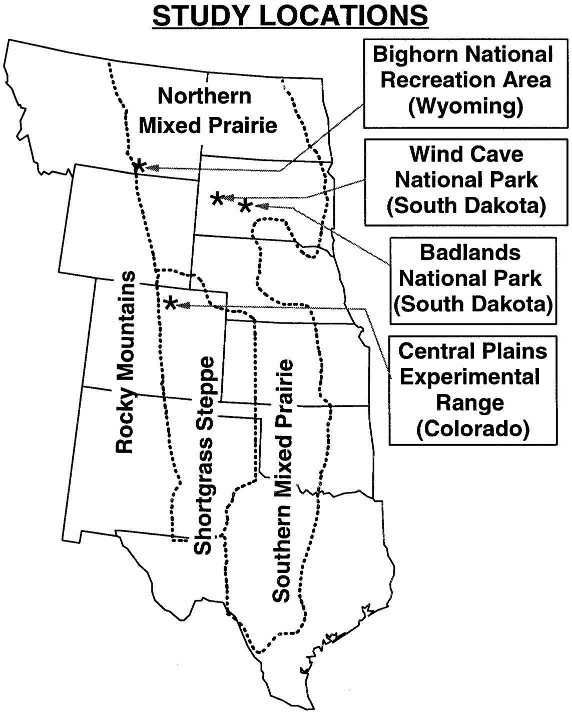

Figure 1. Map of study areas.

Study areas and methods

Study areas

We had four study locations: one in the shortgrass steppe at the 'Central Plains' Experimental Range (Pawnee National Grassland, Colorado) and three areas of northern mixed prairie in 'Wind Cave' National Park (South Dakota), 'Badlands' National Park (South Dakota), and 'Bighorn' Canyon National Recreation Area (Wyoming and Montana; Figure 1, Table 1). Shortened place names in quotes are used hereafter. We randomly established four 20 m × 50 m sample plots in riparian zones (creek sides, kettle ponds, or obvious intermittent drainages) and upland sites at each location. Care was taken to select sites with similar grazing intensities for riparian and upland sites in each area. At Central Plains, all sites were grazed season-long (June-October) by cattle and pronghorn. At Wind Cave, all plots are exposed to grazing by native ungulates (bison, deer, and elk). At Badlands, all areas are grazed by bison, pronghorn antelope, and deer, and areas in those three management areas are also grazed by prairie dogs. Bighorn is grazed by wild horses, bighorn sheep, and deer.

Table 1. Study area descriptions.

Area	Vegetation type	Site type	Elev. (m)	Primary herbivores
Central Plains Experimental Range (Nunn, Colorado)	short-grass steppe	upland riparian	1644 1619	cattle, pronghorn
Wind Cave National Park (Hot Springs, South Dakota)	northern mixed-grass prairie	upland riparian	1244 1187	bison, elk, deer, prairie dogs
Badlands National Park (Interior, South Dakota)	desert mixed-grass	upland riparian	794 783	bison, deer, pronghorn, prairie dogs
Bighorn National Recreation Area (Lovell, Wyoming)	cushion plant / mixed-grass	upland riparian	1353 1161	wild horses, bighorn sheep, deer

Methods

At each of the four study areas, we randomly selected the location of four plots in both riparian and upland sites. Riparian sites included perennial and intermittent streams, and lowland depressions that held water for extended periods (ca 1 month or more). Upland sites were defined as drier sites with similar slopes, aspects, and elevations as riparian sites. A Modified-Whittaker plot (20 m × 50 m; Figure 2) was placed with the long axis parallel to the environmental gradient (modified from Stohlgren et al. 1995). Nested in each plot were ten 0.5 m × 2 m (1 m^2) subplots, two 2 m × 5 m (10 m^2) subplots, and a 5 m × 20 m (100 m^2) subplot. Foliar cover for each species and percent bare ground were estimated to the nearest percent in the ten 1 m^2 subplots, and cumulative plant species were noted in the 10 m^2 and 100 m^2 subplots, and the 1000 m^2 plots. Ancillary data recorded for each plot included: UTM location and elevation from a global positioning system, slope, and aspect.

Each site was sampled as close to the peak plant phenology as possible. We sampled the Central Plains Experimental Range from 9–11 June 1997, Wind Cave National Park from 25–28 June 1997, Badlands National Park from 2–5 July 1997, and Bighorn Canyon National Recreation Area from 25–27 July 1997. Plant species that could not be identified in the field were collected and identified at site and Colorado State University herbaria. About 15% to 18% of the plant species in riparian and upland sites, respectively, could not be identified due to phenological stage and missing flower parts, since all sites were at least moderately grazed.

Five soil samples were taken at the four corners and center of each 1000 m^2 plot, and pooled into one plastic bag. For each sample, surface litter, if present, was removed, and the top 15 cm of soil was sampled. Samples were air-dried for at least 48 h, sieved with a standard #10 (2 mm pore size) sieve, ground in a standard three ball grinder, and then oven-dried at 55 °C for 24 h. Samples were analyzed for percent total carbon and nitrogen using a LECO-1000 CHN Analyzer (following the methods of Carter 1993), and for particle size based on the standard hydrometer method (Gee & Bauder 1986).

Finally, we used Jaccard's coefficient (J) to measure the overlap between the combined species lists of the four riparian and upland plots in each management area (Krebs 1989) as follows:

$$J = A/(A + B + C),$$

where $A =$ the number of species found in both upland and riparian sites, $B =$ species in the upland plots but not in riparian plots, and $C =$ species in riparian plots but not in upland plots. A comparison of species lists for two sites resulting in a similarity coefficient of 1.0 would indicate complete overlap (i.e., identical species lists), while a value of 0.0 would indicate no overlap.

Statistical analysis

All statistical analyses were conducted with SYSTAT (version 6.0, SPSS, Inc.), and $P < 0.05$ was used to determine significance in all tests. T-tests were used to compare the number and foliar cover of native and exotic species, soil characteristics, etc., in riparian versus upland sites. Multiple regression was used to determine the relationship of the number and cover of native plant species in 1 m^2 subplots and 1000 m^2 plots to the number and cover of exotic plant species

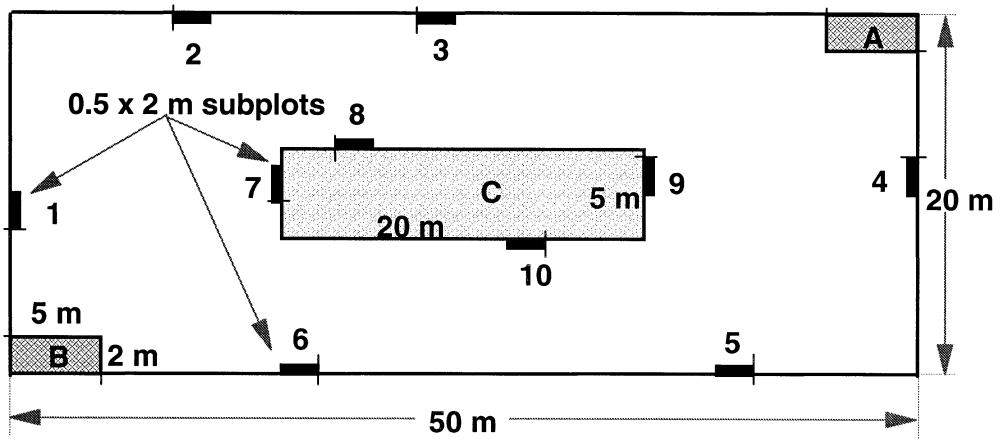

Figure 2. The Modified-Whittaker Plot design (adapted from Stohlgren et al. 1995).

with separate analyses for riparian and upland sites. We tested the significance of each predictor with *t*-values (i.e., against the null hypothesis that the slope $= 0$). We repeated the analysis with combined plot data for each vegetation type (i.e., riparian versus upland types) in each area.

We used stepwise forward multiple regressions to assess the ability of native species richness and cover, and soil characteristics to predict exotic species richness and cover in riparian and upland sites. Soil characteristics included total % N, total % C, % silt, and % clay (% sand was not added into the model to reduce multi-collinearity). The forward linear regression models included only variables meeting the $P < 0.15$ criterion. Data distributions that were strongly skewed were transformed prior to analysis. Log_{10} transformations were used on the cover of exotic species and soil % N.

Results

Local plant species richness and cover in riparian and upland sites

Plant species richness and cover varied considerably among sites (Table 2). Mean exotic species richness in 1 m^2 subplots ranged from 0.02 species m^{-2} (± 0.02 species; 1 S.E.) in upland sites at Central Plains to 3.0 species m^{-2} (±0.3 species) in upland sites at Badlands. Mean native species richness ranged from 4.9 species m^{-2} (±0.3 species) in upland sites at Central Plains to 9.0 species m^{-2} (±0.4 species) in upland sites at Wind Cave in 1 m^2 subplots. The mean foliar cover of native species ranged from 21% to 39% for the study areas. The mean foliar cover of exotic species was negligible (<0.2%) at Central Plains and highest in the riparian sites at Bighorn (18%) and the upland sites at Badlands (almost 22%).

At the 1 m^2 scale, native and exotic plant species richness and foliar cover varied in riparian and upland sites, and there were no consistent patterns among the four management areas (Table 2). For example, for all subplots combined, the foliar cover of native species was significantly greater in riparian zones than in upland sites, but the Central Plains area had higher native species cover in upland sites. Exotic species richness and cover were higher in the riparian zones than upland sites in three of four management areas compared (Table 2).

Many of the relationships between plant species richness and cover, or between riparian and upland sites were highly scale-dependent (Figure 3). For example, the significant negative relationships (at the 1 m^2 and 1000 m^2 scales) between exotic species richness and native plant foliar cover for upland sites were not significant for riparian sites (Figures 3a, 3c). At the vegetation-type scale (i.e., combined data from the eight plots in a management area), there was a significant positive relationship between exotic species richness and native plant foliar cover (Figure 3f).

Vegetation characteristics of upland and riparian sites were far more consistent at the 1000 m^2 scale compared to the 1 m^2 scale (Table 3). Riparian zones had higher richness of native and exotic plant species (and thus total species) than upland sites in each of the management areas. Soil texture, % C, and % N were variable for the sites and management areas, and the ranges of values among areas made it difficult to

Table 2. Mean characteristics in 1 m^2 subplots for upland (Up) and riparian (Rip) sites by area. Standard errors in parentheses.

Characteristics	Area									
	CPER		Wind Cave		Badlands		Bighorn		All Areas	
	Up	Rip	Up	Rip	Up	Rip	Up	Rip	Up	Rip
No. exotic spp.	0.02^{b}	0.15^{b}	1.18^{b}	1.75^{b}	3.00^{a}	1.42^{a}	0.32^{a}	2.18^{a}	1.13^{c}	1.38^{c}
	(0.02)	(0.06)	(0.15)	(0.14)	(0.26)	(0.19)	(0.13)	(0.24)	(0.12)	(0.10)
Exotic cover (%)	0.02^{c}	0.16^{c}	13.08	11.98	21.65^{a}	2.38^{a}	1.18^{a}	18.35^{a}	8.98	8.22
	(0.02)	(0.07)	(2.70)	(1.88)	(4.25)	(0.51)	(0.74)	(3.38)	(1.44)	(1.13)
No. native spp.	4.9^{a}	7.6^{a}	9.0^{b}	7.5^{b}	5.8	5.6	5.8	5.1	6.4	6.5
	(0.3)	(0.5)	(0.4)	(0.5)	(0.3)	(0.3)	(0.4)	(0.4)	(0.2)	(0.2)
Native cover (%)	39.0	31.6	32.5	38.1	22.7^{a}	37.8^{a}	20.6^{a}	38.0^{a}	28.7^{a}	36.3^{a}
	(3.5)	(2.8)	(3.6)	(2.7)	(2.0)	(3.8)	(1.8)	(4.3)	(1.5)	(1.7)
Total No. spp.	4.9^{a}	7.8^{a}	10.2	9.2	8.8^{a}	7.1^{a}	6.1^{b}	7.3^{a}	7.5	7.8
	(0.3)	(0.5)	(0.5)	(0.5)	(0.4)	(0.4)	(0.4)	(0.4)	(0.2)	(0.2)
Total cover (%)	39.0	31.7	45.6	50.0	44.4	40.1	21.7^{a}	56.4^{a}	37.7^{a}	44.6^{b}
	(3.5)	(2.8)	(2.7)	(3.4)	(4.4)	(3.8)	(1.9)	(4.3)	(1.8)	(1.9)
No. subplots (*n*)	40	40	40	40	40	40	40	40	40	160

Means within areas with superscript ^{a} , superscript ^{b} , or superscript ^{c} are significant at $p < 0.001$, $p < 0.05$, and $p < 0.10$, respectively.

evaluate grand mean values for the four management areas. However, for all areas combined, the significantly greater ($P < 0.05$) exotic species richness in riparian zones generally coincided with greater overall plant diversity and higher ratios of C to N in the soil (Table 3).

Landscape-scale plant species richness and cover in riparian and upland sites

We assessed landscape-scale relationships in plant species richness and cover by combining data across sites and management areas. We found that some aspects of species richness and cover were more predictable than others (Table 4). For all 32 plots combined, only 21% of the variance in exotic species richness was explained by soil % silt and total foliar cover. Likewise, 26% of the variance in exotic species cover ($\log_{10}$ cover) was explained by soil % silt and total plant species richness. There was also a positive significant correlation between soil % silt and soil clay ($r = 0.38$, $P = 0.03$), so it appears that exotic species in the four study areas establish more successfully in soils with greater water holding capacity.

Total species richness and cover were more predictable. About 44% of the variance in total species richness was explained by positive relationships with total foliar cover and soil C:N. Meanwhile, 48% of the variance in total foliar cover was explained by positive relationships with total species richness and soil % N, and a negative relationship with soil C:N. It was surprising to find that the best predictors of native species cover at landscape scales included exotic species richness and exotic species cover (Table 4).

For additional landscape-scale analyses, we treated the four replicate 1000 m^2 plots in either upland or riparian sites in each management area as separate vegetation types. We also found that exotic species readily invaded areas high in plant diversity, foliar cover, and total soil nitrogen (Figure 4). The most significant positive relationships were between total foliar cover and exotic species richness, total foliar cover and exotic species cover, and exotic species richness and cover.

At landscape scales, riparian zones were found to be particularly rich in native and exotic plant diversity in the four management areas (Table 5). About 26% more native plant species were found in riparian sites compared to upland sites at the four study areas. On average, we found that 85% (±5%) of the exotic species in the eight sampling plots in a given management area could be found in riparian zones, significantly more ($P < 0.017$; *t*-test) than in upland

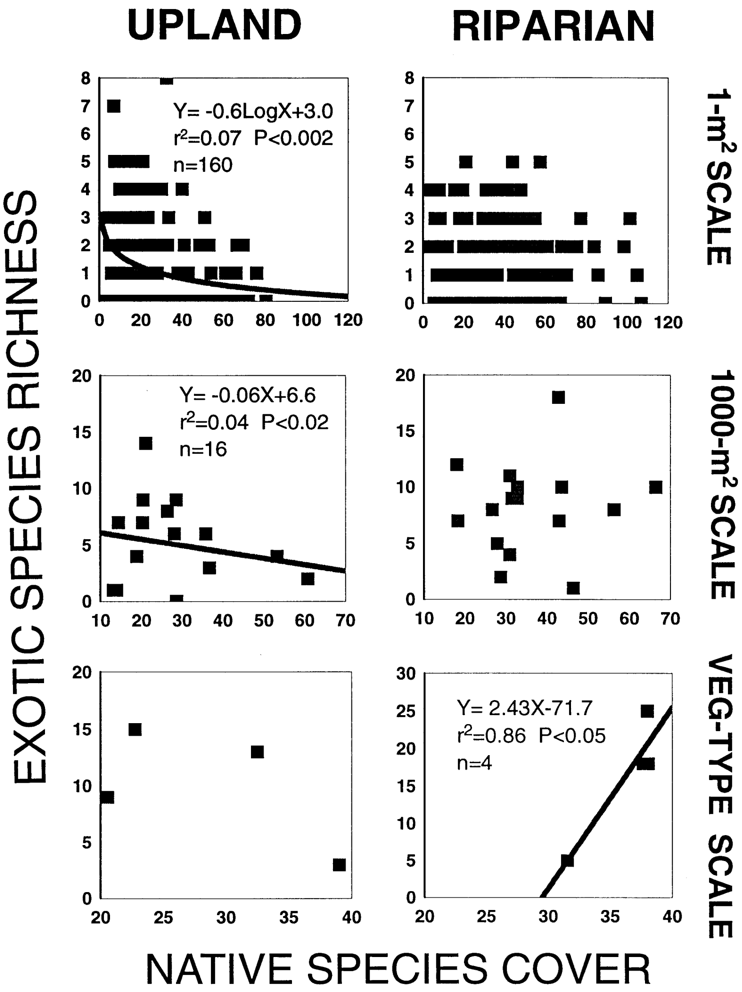

Figure 3. Relationship of exotic species richness at multiple spatial scales to native species cover (from 1 m^2 subplots) for upland and riparian sites in the four study areas. Coefficients of determination and significance levels of linear and non-linear regressions are shown where they are significant.

plots which had only 50% (±8%) of the exotic species recorded. We also found, on average, that 80% (±3%) of the total species recorded in the eight sampling plots in a management area could be found in riparian zones. This was also significantly more ($P < 0.005$) than in upland plots which recorded 59% (±3%) of the total plant species recorded in a given management area (Table 5).

We found that species composition overlap between upland and riparian sites ranged from 47% overlap at Central Plains to only 25% species overlap at Bighorn (Table 6). Only about 13% to 26% of the plant species recorded were unique to upland sites in a given management area.

Discussion

Generalizations

Placing plots in riparian zones was an efficient way to rapidly assess native and exotic plant diversity in the four management areas (Table 5) primarily for two reasons. First, the 20 m × 50 m plot was large enough to sample the riparian zone and the fringes of upland areas. Second, both native and exotic plant species appear to prefer environments with plenty of light, water, and nitrogen (Table 4, Figure 3). Mean total foliar cover averaged only 48% (±5%) in the 32 plots, suggesting that grazing and other disturbances help to maintain high light levels reaching vegetation and reduce above-ground competition (Stohlgren et

Table 3. Mean characteristics in 1000 m^2 plots for upland (Up) and riparian (Rip) sites by area. Standard errors in parentheses. $n = 4$ plots each.

Characteristics	Area									
	CPER		Wind Cave		Badlands		Bighorn		All Areas	
	Up	Rip	Up	Rip	Up	Rip	Up	Rip	Up	Rip
No. exotic spp.	1.0 (0.6)	3.0 (1.1)	6.2^{c} (0.9)	9.0^{c} (0.9)	9.0 (1.5)	9.5 (0.6)	2.7^{a} (1.9)	9.5^{a} (2.7)	4.8^{b} (1.0)	7.8^{b} (1.0)
No. native spp.	33.0 (2.7)	44.5 (9.6)	50.2 (6.5)	56.5 (5.4)	26.0 (2.2)	33.0 (5.5)	23.7 (1.5)	29.0 (4.5)	33.2 (3.2)	40.8 (4.0)
Total No. spp.	34.0 (2.6)	47.5 (10.4)	60.5^{c} (7.3)	74.5^{c} (5.8)	35.0 (3.0)	42.5 (5.4)	26.5 (3.3)	38.5 (6.1)	39.0^{c} (3.9)	50.8^{c} (4.9)
Sand %	72.6^{b} (3.4)	56.7^{b} (4.2)	23.1 (2.1)	61.4 (2.9)	24.2 (5.0)	28.0 (8.3)	53.5 (4.7)	62.1 (8.6)	43.4 (5.7)	52.0 (4.6)
Silt %	6.06^{b} (1.4)	14.6^{b} (1.7)	31.9^{b} (2.4)	15.1^{b} (2.9)	30.4 (5.2)	25.6 (2.5)	12.0 (5.2)	13.5 (6.2)	20.1 (3.4)	17.2 (2.1)
Clay %	21.3 (2.2)	28.7 (4.8)	45.0^{b} (0.9)	23.5^{b} (4.4)	45.3 (8.2)	46.5 (8.6)	36.6^{c} (4.7)	24.5^{c} (2.7)	37.1 (3.3)	30.8 (3.5)
C %	0.76 (0.09)	0.93 (0.21)	3.32 (0.85)	2.80 (0.11)	1.54 (0.16)	1.53 (0.05)	2.19 (0.63)	0.84 (0.21)	1.95 (0.34)	1.52 (0.21)
N %	0.08 (0.01)	0.09 (0.02)	0.24 (0.05)	0.19 (0.02)	0.14 (0.01)	0.10 (0.02)	0.16 (0.05)	0.11 (0.06)	0.16 (0.02)	0.12 (0.02)
C/N	9.6 (0.6)	11.5 (1.3)	13.2 (1.9)	15.8 (2.4)	11.2 (0.8)	18.0 (4.0)	16.5^{c} (1.9)	9.5^{c} (2.2)	12.4 (0.9)	14.0 (1.5)

Means within areas with superscript ^{a} , superscript ^{b}, or superscript ^{c} are significant at $p < 0.001$, $p < 0.05$, and $p < 0.10$, respectively.

al. 1998c). The positive relationships between exotic species richness (and cover) to soil % silt (Table 4), between soil % silt and % clay, and between exotic species cover and soil % N (Figure 3), probably indicate increased soil water holding capacity and nitrogen availability in high-diversity, high-cover sites.

Our results strongly corroborate a native and exotic plant survey in four prairie types in the Central Grasslands and five forest and meadow vegetation types in the Colorado Rockies (Stohlgren et al. 1998a). In that study, exotic species cover was positively correlated to total foliar cover, mean soil % N , and the total number of exotic species. Planty-Tabacchi et al. (1996) also reported higher invasibility in species-rich riparian zones in southwest France and in the northwestern United States compared to upland sites. As found in our study, species-rich sites had greater percentages of exotic species in the flora. Other studies have also reported exotic species invasions of species-rich riparian zones (Fox & Fox 1986; Macdonald et al. 1986; Crawley 1987; Malanson 1993; DeFerrari & Naiman 1994). However, general patterns of invasibility remained elusive in those studies because each used different methods and scales of measurements.

The scale of measurement greatly influenced the assessment of exotic plant species invasion. For example, the almost significant negative relationship between exotic species richness and native species cover at the 1 m^2 scale in riparian sites (coefficient $= -0.006$, $t = -1.65$, $P = 0.099$), was a significant positive relationship at the vegetation-type scale (Figure 2). In this study, we found positive relationships between total plant species cover and exotic species richness at the 1 m^2 scale (coefficient $= 0.022$, $t = 6.83$, $P = 0.001$), 1000 m^2 plot scale (coefficient $= 0.07$, $t = 2.6$, $P = 0.014$) and landscape scale (coefficient $= 0.49$, $t = 2.6$, $P = 0.041$). However, the slope of the line at the 1 m^2 scale was near zero, and in a similar study in the Central Grasslands, we found significant negative relationships between exotic species richness and total foliar cover at the 1 m^2 scale, and positive relationships at larger scales

Table 4. Multiple linear regressions of species richness and cover, and soil characteristics as predictors of exotic, native, and total species richness and cover for the 32 1000 m^2 plots in the study.

Dependent variable	Predictors	Coef.	t	P	Model F	Model P	Model R^2
No. exotic Species	Soil% Silt	0.105	1.74	0.054	5.2	0.012	0.21
	Total Foliar Cover%	0.062	2.43	0.022			
Log $_{10}$ cover Exotic species	Soil% Silt	0.017	2.32	0.27	6.4	0.05	0.26
	No. Total Species	0.12	2.46	0.20			
No. native Species	Total Foliar Cover %	0.28	3.00	0.006	5.7	0.009	0.24
	Soil C:N	1.08	2.11	0.044			
Cover native Species	Soil C:N	1.39	2.05	0.051	4.1	0.017	0.24
	No. Exotic Species	−0.61	−2.72	0.011			
	Cover Exotic Species	−1.51	−3.02	0.006			
No. total species	Total Foliar Cover %	0.453	4.58	0.001	12.3	0.001	0.44
	Soil C:N	1.534	2.79	0.009			
Total foliar Cover %	Soil C:N	−1.78	−2.27	0.032	10.1	0.001	0.48
	No. Total Species	0.84	4.02	0.001			
	Soil % N	99.81	2.10	0.045			

(Stohlgren et al. 1998a). Thus, sampling only with sets of 1 m^2 plots may be masking the more important finding for land managers that exotic species are invading those portions of landscapes that are high in total foliar cover.

The data from multiple-scales are complementary rather than contradictory. We propose that within vegetation types and habitats that are high in foliar cover, smaller microhabitats relatively lower in foliar cover are invaded by exotic species. Meanwhile, the rate that exotic species are encountered exceeds the rate that native species are added to the species pool as plot size increases or as additional plots are surveyed (Stohlgren et al. 1998a). At the 1 m^2 scale, there were no consistent patterns among all management areas in native and exotic species richness and foliar cover varied in riparian and upland sites (Table 2). More consistent relationships were found at the 1000 m^2 plot scale (Table 3) and at the landscape scale (Figure 3). Assessing the patchy distribution of the many exotic species may require multi-scale sampling techniques because it is likely that different processes of invasion are working at different scales (Stohlgren et al. 1998a–c). Small-plot survey data and experiments (e.g., Tilman 1997) may help to understand microsite processes, while large-plot surveys help understand and predict landscape-scale patterns of native and exotic plant diversity (Stohlgren et al. 1997a–c, 1998a–c).

Habitat-specific and species-specific field observations

Sweeping generalizations in ecology are often challenged with specific observations, and this study is no exception. The generality that riparian zones are prone to invasion by exotic species is challenged at Badlands due to two exotic annual grass species: *Bromus tectorum* L. and *Bromus japonicus* Thunberg. Although these two species averaged $<2\%$ foliar cover in riparian plots in all four study areas, three of four upland plots at Badlands had high % cover of these species (*B. tectorum* L. $=$ 5.7% and *B. japonicus* Thunberg $=$ 12.7% in Plot 1; *B. japonicus* Thunberg $=$ 4.9% in Plot 2; *B. tectorum* L. $=$ 27.8% and *B. japonicus* Thunberg $=$ 10.9% in Plot 4). We think this is due to the species-specific requirements for these annual grasses, their natural patchy distribution, and their competitive advantage in upland habitats. Conversely, these factors may favor exotic forb species in riparian zones in this area. Exotic forbs (e.g., *Sisymbrium*

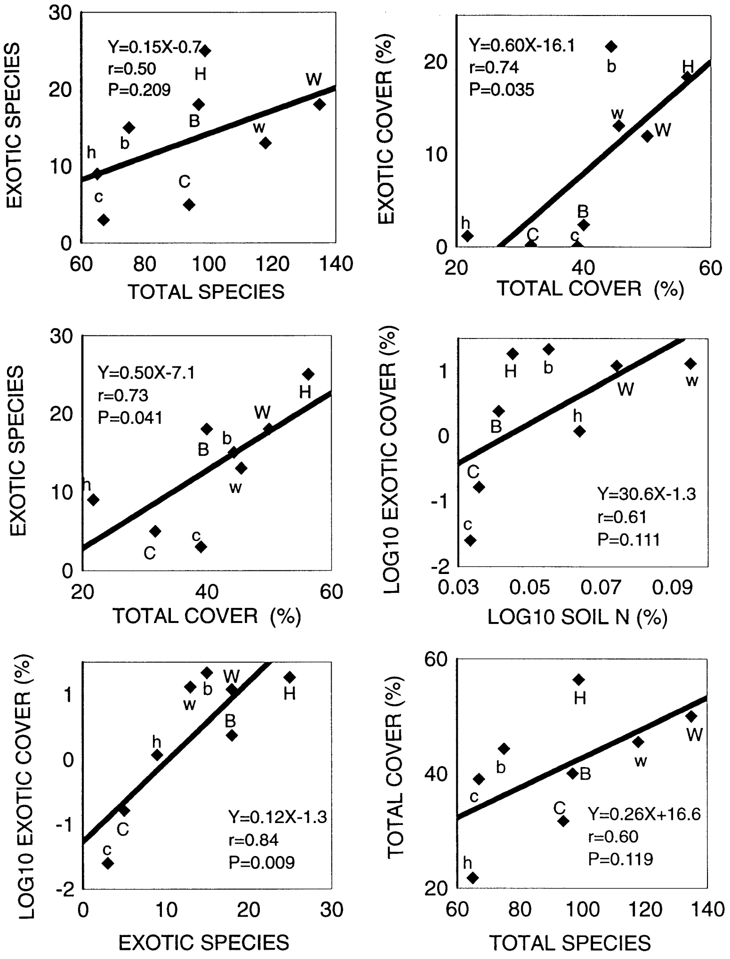

Figure 4. Relationships of species richness and cover at landscape-scales (data combined from four 1000 m^2 plots per area and site-type). Capital letters are used for riparian sites where C = Central Plains, B = Badlands, H = Bighorn, and W = Wind Cave. Lower case letters are for upland sites, respectively.

altissimum L., *Cirsium arvense* (L.) Scop., *Salsola iberica* Sennen & Pau) also dominated riparian sites at Bighorn.

Generalizations about high exotic plant cover in riparian area are also challenged at Wind Cave. *Poa pratensis* L., a sod-forming perennial exotic grass, was found to be a habitat generalist in this area. It was one of the five most dominant species in two upland plots and three riparian plots. *P. pratensis* L. seems to maintain itself well in grazed landscapes once established in either riparian or upland sites (Stohlgren et al. 1998a, c).

The species-specific exceptions do not negate the benefits of the generalizations above. As seen in the case of *P. pratensis* L. at Wind Cave, we could predict that both riparian and upland sites would be invaded by exotic plant species that tend to be habitat generalists. However, we would still expect higher exotic species richness in riparian zones than upland sites, particularly at the 1000 m^2 scale and the landscape level (Tables 3 and 5).

Relationship to ecological theory

We now focus our attention back to the two major opposing theories on the invasibility of plant communities. Elton (1958) stated that exotic species might more easily invade areas of low species diversity because areas of high species diversity should use limiting resources more completely, preventing invasion by a potentially competing species (MacArthur & Wilson 1967; Tilman 1982, 1997; Pimm 1991; McNaughton 1983). The alternate theory by May (1973) and Huston

Table 5. Species richness in four 1000 m^2 plots (duplicate species removed) in upland, riparian, and combined sites in four study areas.

Area	Site	No. native spp.	No. exotic spp.
Central plains	Upland	63	3
	Riparian	89	6
	Combined	100	8
Wind cave	Upland	105	13
	Riparian	114	18
	Combined	117	23
Badlands	Upland	61	15
	Riparian	80	19
	Combined	101	20
Bighorn	Upland	56	9
	Riparian	76	24
	Combined	105	25

Table 6. Number of species in riparian, upland, and both sites and species composition overlap ($J \times 100$) for the four study areas.

Area	Number of species in			Species overlap (%)	Total species
	Both sites	Upland sites only	Riparian sites only		
Central Plains	51	14	43	47.2%	108
Badlands	52	21	46	43.7%	119
Bighorn	32	32	65	24.8%	129
Wind Cave	72	46	60	40.4%	178

and DeAngelis (1994) is that highly diverse plant communities are intrinsically unstable with some species dropping in and out routinely.

Our data weakly supported Elton's theory at the 1 m^{2}scale, and strongly supported the theories of May (1973) and Huston and DeAngelis (1994) at plot-, vegetation type-, and landscape-scales. At subplot (1 m^2) scales, we found a significant negative relationship between exotic species richness and native species cover in upland sites (Figure 3a) as would be predicted by Elton's theory. However, our vegetation type- and landscape-scale results (Figures 3 and 4, Tables 3 and 5) strongly suggest that many species-rich, high-cover areas may be particularly invasible. Combined with similar results from riparian zones and riverine habitats (Fox & Fox 1986; Macdonald et al. 1986; Crawley 1987; Malanson 1993; DeFerrari & Naiman 1994; Ferreiro & Moreira 1995; Planty-Tabacchi et al. 1996), there is a growing body of evidence that many species-rich areas are havens for exotic plant species.

Huston and DeAngelis (1994) realized the distinction between local and regional effects on plant diversity. We found that relationships at one scale, such as the relationship between native species cover and exotic species richness, can completely reverse at a larger scale. At very small scales, i.e., plant neighborhoods, exotic species establish in low diversity, low foliar cover, high bare ground microsites. At vegetation-type and landscape scales, the general habitats are likely high in foliar cover, plant diversity (i.e., native and exotic species), and available resources (light, water, and nutrients). We hypothesize that even areas with high species richness and cover are likely to have unused (available) resources (Fox & Fox 1986) in the presence of grazing and frequent small-scale disturbances from rodents and mechanical impacts on soil by livestock and wildlife. We also suspect that many low-diversity natural systems (e.g., the Central Plains site; Tables 2, 3, 5, Figure 4) are resistant to invasion because: (1) they have low levels of total resources such as soil nutrients and water availability; or (2) the native plant species in those systems monopolize available resources to resist invasion (also see Stohlgren et al. 1998a).

Maximum species richness (native and exotic species) should coincide with moderate levels of productivity (Huston 1992; Huston & DeAngelis, 1994). In the grasslands we studied, however, grazing and disturbance (periodic flooding, rodent digging, fire), may keep foliar cover values low enough (ca 50%) that even the 'high' cover end of the spectrum could have some available resources (such as light, water, and nutrients) for invading species.

Theories linking intermediate disturbances to diversity would suggest that fire, flooding, and grazing, would likely contribute to the high diversity in many ecosystems (Caswell 1978; Connell 1978; Petraitis et al. 1989). In grasslands, fire may be more important in upland sites (dry fine fuels), flooding may be more important in riparian zones (Edwards et al. 1995; Brambley et al. 1995), and grazing and rodents are common to both sites (Stohlgren et al. 1998c). The effects of disturbance were beyond the scope of this study. However, a recent analysis of 26 long-term exclosure sites in Colorado, Wyoming, Montana, and South Dakota found no evidence that grazing or cessation from grazing caused significant differences in native and exotic species richness, and the cover of exotic species (Stohlgren et al. 1998c). Thus, in these areas, periodic flooding in riparian zones, drought in upland sites, and other disturbances likely contribute more to patterns of plant diversity than do differences in grazing pressure (except where mechanical damage is high or where severe erosion occurs).

Management Implications

Riparian zones are lifelines throughout otherwise arid grasslands which may make them ‘corridors of invasion.’ Sýkora (1990) reported that two-thirds of the Polish exotic flora could be found in riverine habitats. In our study, 85% of the exotic plant species that we encountered could be found in riparian zones. This is an obvious concern for resource managers. Many studies have shown exotic plants spreading from foci (e.g., Mack 1981; Kareiva 1990; Bergelson et al. 1993). The spread of exotic species within riparian zones may be aided by contiguous, often linear or branching habitat where dispersal of seeds by water is common. Riparian zones may also act as ‘source’ populations (Pulliam 1988 in a broader sense) of exotic species, poised for the invasion of nearby upland sites when conditions are favorable. Thus, the connectivity of the corridors may have profound negative effects on the ecosystem: usually the positive aspects of migratory and habitat corridors are stressed (see Primack 1993). Our casual observations suggest that the disturbed shoulders of roads which often cross riparian zones are also corridors for exotic plant species.

Natural areas serve as index sites of large-scale environmental change and monitors of exotic plant species invasion within a region (Vitousek et al. 1996). It now appears that riparian zones may serve as index sites within the natural areas. Species overlap comparisons of riparian and upland plots showed that about one-third to one-half the species found in riparian zones were unique to those sites. Less than 25% of the plant species found in upland sites were unique to those sites. However, our subjective classification of ‘riparian’ and ‘upland’ sites was not as important as the overriding patterns at landscape scales: (1) high-fertility or excessively disturbed upland sites may be equally invasible as some riparian sites; and (2) rapid assessments should target riparian zones and high fertility/excessively disturbed sites. As was found in a previous study in the Colorado Rockies and the Central Grasslands (Stohlgren et al. 1998a), areas of high native plant species richness and cover (Table 2) and areas high in soil fertility (Table 2, Figure 3) in natural landscapes may be highly invasible. These sites are usually hot spots of biological diversity, rare habitats with distinctive plant and animal communities (Stohlgren et al. 1997a,b; Stohlgren et al. 1998a).

Highly invasive exotic plant species will likely cause a decline in native plant species and ecosystem diversity (Bock et al. 1986; Billings 1990; D’Antonio & Vitousek 1992). Exploratory, quantitative inventory and monitoring should be initiated immediately to assess the status and trends of invading plants across scales in selected natural areas. Because small populations of exotic plant species can spread quickly over the landscape (Mack 1981), their early detection is crucial to land managers (Stohlgren et al. 1998b). Standardized approaches to inventory and monitor invasive species (Stohlgren et al. 1997a,b, 1998a) and understanding their effects on natural systems (Everitt et al. 1995) are precursors to control measures. Both species-specific data and habitat-specific information must be collected (e.g., Moulton & Pimm 1986; D’Antonio 1993; Lodge 1993). Since the factors influencing exotic species establishment (small-scale dynamics; Figure 3) may be different than those influencing landscape-scale exotic species dynamics (Figures 3 and 4), we suggest that the processes of initial invasion and naturalization be studied in separate but integrated ways (Stohlgren et al. 1998a). Integrated studies of plant ecology are urgently needed where exotic species invade and dominate. Control efforts may be urgent, especially for noxious weeds and those that greatly alter natural processes over large areas. However, resource managers must also recognize the high native biodiversity in many infested areas, and the potential dangers of some control measures (poisons, herbicides) in or near riparian zones.

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