DOI: 10.1007/s00267-001-0006-2

Assessing Vulnerability to Invasion by Nonnative Plant Species at Multiple Spatial Scales

THOMAS J. STOHLGREN*
GENEVA W. CHONG
Midcontinent Ecological Science Center
U.S. Geological Survey
Fort Collins, Colorado 80525, USA

LISA D. SCHELL
KELLY A. RIMAR
YUKA OTSUKI
MICHELLE LEE
MOHAMMED A. KALKHAN
CYNTHIA A. VILLA
Natural Resource Ecology Laboratory
Colorado State University
Fort Collins, Colorado 80523-1499, USA

ABSTRACT / Basic information on where nonnative plant species have successfully invaded is lacking. We assessed the vulnerability of 22 vegetation types (25 sets of four plots in nine study areas) to nonnative plant invasions in the north–central United States. In general, habitats with high native species richness were more heavily invaded than species-poor habitats, low-elevation areas were more invaded than high-elevation areas, and riparian zones were more invaded than nearby upland sites. For the 100 1000-m^2 plots (across all vegetation types), 50% of the variation in nonnative species richness was explained by longitude, latitude, native plant species richness, soil total percentage nitrogen, and mean maximum July temperature ($n = 100$ plots; $P < 0.001$). At the vegetation-type scale ($n = 25$ sets of four 1000-m^2 plots/type), 64% of the variation in nonnative species richness was explained by native plant species richness, elevation, and October to June precipitation ($P < 0.001$). The foliar cover of nonnative species (log) was strongly positively correlated with the nonnative species richness at the plot scale ($r = 0.77$, $P < 0.001$) and vegetation-type scale ($r = 0.83$, $P < 0.001$). We concluded that, at the vegetation-type and regional scales in the north–central United States, (1) vegetation types rich in native species are often highly vulnerable to invasion by nonnative plant species; (2) where several nonnative species become established, nonnative species cover can substantially increase; (3) the attributes that maintain high native plant species richness (high light, water, nitrogen, and temperatures) also help maintain nonnative plant species richness; and (4) more care must be taken to preserve native species diversity in highly vulnerable habitats.

Invasive nonnative plant species are a growing concern in the north–central United States and elsewhere because some of them can poison livestock, clog waterways, compete with cash crops, and degrade rangelands (Westbrooks 1999). In this paper, we operationally define nonnative species as species from other continents. Managers of national parks, wildlife refuges, and other natural areas are also concerned because of the potential negative effects of nonnative plant species on native plant diversity, wildlife habitat, native pollinators, fire regimes, and nutrient cycling (Vitousek 1990, D'Antonio and Vitousek 1992, Stohlgren and others 1999a, Westbrooks 1999). Thus, there is an urgent need to assess the vulnerability of natural landscapes and specific habitats to invasion (Loope and Mueller-Dombois 1989). To guide research, control, and restoration efforts, basic information is needed on where nonnative species have successfully invaded. Since only a small portion of any large landscape or region can be affordably surveyed, modeled information on native and nonnative plant diversity, soil characteristics, topography, and climate is needed to guide the management of invasive species in the larger, unsampled areas (Stohlgren and others 1997, Chong and others 2001).

Little is known about the vulnerability of many natural landscapes to invasion (Alpert and others 2000). Global-scale observations, ecological theory, and small-scale experiments may not be particularly helpful. Observations from Darwin (1859) and Elton (1958) to Vitousek and others (1996) and Rejmánek (1996) clearly show that species-poor plant communities on islands are easily invaded by nonnative plant species. Observations also show that species-rich tropical rain forests have been poorly invaded by nonnative species (Elton 1958, Rejmánek 1996). In a recent synthesis of floras around the globe, Lonsdale (1999) found that many species-rich areas had high numbers of nonnative

KEY WORDS: Nonnative species richness; Habitats vulnerable to invasion; Native plant diversity; Soil and climate characteristics

---

*Author to whom correspondence should be addressed; *email:* Tom_Stohlgren@USGS.gov species, and scientists are questioning earlier theories and paradigms (Stohlgren and others 1999a, Levine and D'Antonio 1999). Still, there are few generalities about plant invasion in various vegetation types over large continental areas (Moulton and Pimm 1986, Crawley 1987, Rejmánek 1996).

Several mathematical models suggest that areas of high species diversity should be resistant to invasion by nonnative species (Turelli 1981, Post and Pimm 1983, Rummel and Roughgarden 1983, Case 1990, Law and Morton 1996). The mathematical models generally claim that colonization by nonnative species should decline in the face of many strongly interacting species, which are thought to use resources more completely. A few field studies and small-scale experiments have reported a negative relationship between native and nonnative species richness (Fox and Fox 1986, Smallwood 1994, Tilman 1997). One small-scale experiment (Levine 2000) found a positive relationship between nonnative species success and native plant diversity in one vegetation type in California. In a seed-addition experiment in mature oak savanna in Minnesota, Tilman (1997) found that invasibility correlated negatively with plant species richness ($n = 60$, 1-m^2 plots). Many of these observations, theories, and small-scale experiments could lead land managers to believe that species-rich plant communities might somehow be less vulnerable to invasion by nonnative plants than species-poor communities because there might be no available niches (Grime 1973, MacArthur and Wilson 1967, Tilman 1982, 1997, McNaughton 1983, 1993).

However, a growing number of observational studies have demonstrated that, locally, not all species-rich vegetation types are immune to nonnative plant invasions. Robinson and others (1995) and Robinson and Quinn (1988) showed that species-rich areas of annual grasslands in California were more easily invaded than species-poor areas. Timmins and Williams (1991) found that the number of weeds in New Zealand's forest and scrub reserves did not correlate with the number of native species. Recently, our survey of five forest and meadow vegetation types in the Colorado Rockies and four prairie types in Colorado, Wyoming, South Dakota, and Minnesota reported more extensive nonnative plant invasions in species-rich vegetation types (Stohlgren and others 1999a). Our observations were limited to nine vegetation types (four 1000-m^2 study plots per type), but they raise the possibility that, at a local scale, some species-rich vegetation types could be invaded. To guide research, control, and restoration activities at landscape and regional scales, additional systematic surveys were badly needed to provide land managers with information on the patterns and environmental factors associated with the successful invasion of nonnative plant species.

It is important to understand how studies of plant invasion may be affected by scale (or grain, or plot size) and extent (range of habitats or vegetation types studied, area of the region assessed). Recent small-scale, site-specific experiments have yielded contradictory results showing that species-rich areas can be either less invaded (Tilman 1999) or more invaded (Levine 2000), while global-extent studies suggest that species-rich areas have been heavily invaded (Lonsdale 1999). The results of small-scale experiments and evaluations of regional floras have not been particularly useful to land managers who demand landscape-scale information on which vegetation types are (or may be) heavily invaded. Are some vegetation types consistently more heavily invaded than other habitats. It remains a top research priority of several land management agencies to conduct systematic surveys at multiple spatial scales (e.g., the plot, landscape, and biome-scales) for the early detection and management of nonnative plants.

The objective of this present study was to assess patterns of nonnative plant invasions relative to vegetation-type characteristics, topography, level of disturbance, and soil characteristics (e.g., soil texture, nitrogen, and carbon). We synthesized data from several studies that used the same multiscale vegetation and soil sampling methods to expand greatly the number and spatial distribution of samples compared to single, smaller studies. We developed explanatory models based on the data from the 22 vegetation types throughout the north–central United States from four previous studies (Stohlgren and others 1998a,b, 1999a,b).

Study Areas

Four studies were conducted in nine areas (25 sets of four plots in 22 vegetation types) between 1995 and 1998 (Figure 1). At each site, four multiscale 20 × 50-m vegetation plots (modified Whittaker plots; Stohlgren and others 1995) were sampled as described below.

Grassland Study. Our study locations included shortgrass steppe at the Central Plains Experimental Range (Pawnee National Grassland, Nunn, Colorado), mixed grass prairie at the High Plains Experiment Station (Cheyenne, Wyoming), northern mixed prairie at Wind Cave National Park (Hot Springs, South Dakota), and tallgrass prairie at Pipestone National Monument (Pipestone, Minnesota). Except for the tallgrass prairie location, which had no grazing, we randomly established four 20 × 50-m sample plots at each location that encompassed various grazing intensities including lightly grazed, heavily grazed, and protected habitats.

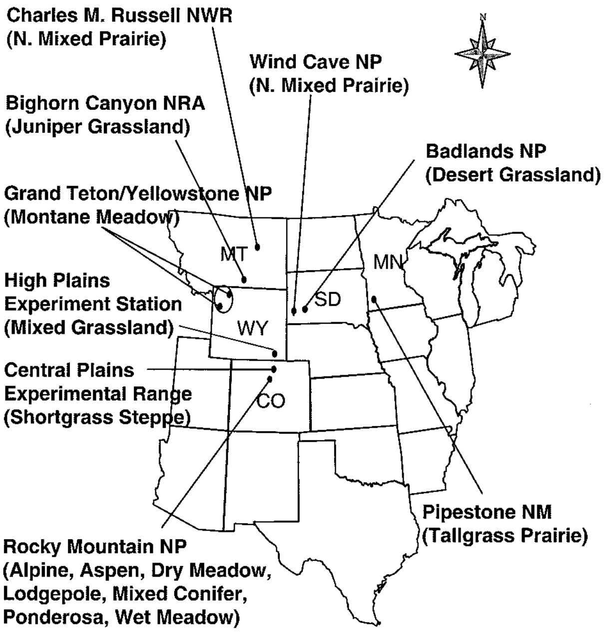

Figure 1. Map of study sites.

At the Central Plains Experimental Range, all sites were grazed, although plot 3 was part of an exclosure that had been opened to grazing in 1990. At the Cheyenne High Plains Experimental Station, three of four plots were grazed primarily by cattle and lightly by native ungulates, while one plot excluded cattle grazing (called "ungrazed"). At Wind Cave National Park, all four plots were located in areas grazed by native ungulates (bison, *Bison bison*; pronghorn, *Antilocarpa americana*; deer, *Odocoieus* spp.; and elk, *Cervus elaphus*). At Pipestone National Monument, all areas are prescribed burned on a 3- to 4-year cycle. In 1996, we sampled the shortgrass steppe from 1 to 3 July, the mixed grass prairie from 25 to 27 June, the northern mixed prairie from 10 to 13 July, and the tallgrass prairie from 24 to 27 July. Plant species that could not be identified in the field were collected and identified at the Colorado State University herbarium. About 9% of the plant specimens collected could not be identified to species due to inappropriate phenological stage or missing flower parts. For more details see Stohlgren and others (1998a).

Riparian Study. There were four study locations: one in the shortgrass steppe at the Central Plains Experimental Range and three areas of northern mixed prairie at Wind Cave National Park (South Dakota), Badlands National Park (South Dakota), and Bighorn Canyon National Recreation Area (Wyoming and Montana). We randomly established four 20×50-m sample plots in lowland/riparian zones along creek sides, kettle ponds, or obvious intermittent drainages and at upland sites at each location. We selected sites with similar grazing intensities for riparian and upland sites in each area. At the Central Plains Experimental Range, all sites were grazed season-long (June–October) by cattle. At Wind Cave National Park, all sites were grazed by native ungulates (bison, deer, and elk). At Badlands National Park, all areas were grazed by bison, pronghorn antelope, deer, and prairie dogs (*Cynomys* spp). Bighorn Canyon National Recreation Area was grazed by wild horses (*Equus caballus*), bighorn sheep (*Ovis Canadensis*), and deer. Each site was sampled as close to peak phenology as possible. In 1997, we sampled the Central Plains Experimental Range from 9 to 11 June, Wind Cave National Park from 25 to 28 June, Badlands National Park from 2 to 5 July, and Bighorn Canyon National Recreation Area from 25 to 27 July. Plant species that could not be identified in the field were collected and identified at the Colorado State University herbarium. About 15 to 18% of the plant species in riparian and upland sites, respectively, could not be identified due to phenological stage or missing flower parts, due to grazing. For more information see Stohlgren and others (1998b).

Rocky Mountain National Park Study. Seven vegetation types were sampled in a portion of Rocky Mountain National Park, Colorado (elevation, 2500–3660 m). These were lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), ponderosa pine (*Pinus ponderosa*), wet meadow (dominated by *Poa palustris, Deschampsia caespitosa,* and *Poa interior*), dry meadow (dominated by *Carex helianthus* and *Artemisia tridentata*), mixed conifer (may include *Abies lasiocarpa, Picea engelmanii, Pinus contorta,* and *Pinus flexilis*), and alpine tundra. Most of the area was moderately grazed by elk and deer. Four 20×50-m sample plots were randomly located in each vegetation type. Each site was sampled as close to the phenological maximum (peak biomass) as possible. Sites at Beaver Meadows, Rocky Mountain National Park, were sampled between 1 June and 15 July 1995 (for details see Stohlgren and others 1997a, 1999a).

Grazing Study. Four modified Whittaker plots in grazed and long-term ungrazed (>12 years of continued protection) areas were sampled at the Charles M. Russell National Wildlife Refuge, Montana, Yellowstone/Grand Teton National Parks, Wyoming, and Wind Cave National Park, South Dakota, in 1996. Yellowstone/Grand Teton National Park was sampled from 9 to 19 July, Wind Cave National Park was sampled from 10 to 12 July, and Charles M. Russell National Wildlife Refuge was sampled from 6 to 11 August. All but 5% of the specimens encountered could not be identified to species. For additional details, see Stohlgren and others (1999b).

Methods

The modified Whittaker sampling plot measured 20 × 50 m (Stohlgren and others 1995) and was placed with the long axis parallel to the environmental gradient. Nested in each plot were 10 0.5 × 2-m (1-m^2) subplots systematically spaced along the inside border. Foliar cover for each species in the understory and percentage bare ground were estimated to the nearest percent in the 10 1-m^2 subplots, and native and nonnative plant species were noted in each 1000-m^2 plot. Ancillary data recorded for each plot included UTM location from a global positioning system and elevation, slope, and aspect.

All plots were rated for disturbance as follows: 0 = long-term exclosure; 1 = almost no grazing by native ungulates or livestock; 2 = light grazing; 3 = moderate grazing; 4 = heavy grazing or mowing; and 5 = recent fire (past 3 years). Five soil samples (0–15 cm deep) were taken from the four corners and center of each plot and pooled into one plastic bag. Surface litter, if present, was removed. Samples were air-dried for 48 h, sieved with a standard No. 10 (2-mm-pore size) sieve, and ground in a standard ball mill grinder. Samples were analyzed for percentage 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 of Gee and Bauder (1986).

Climate data were gathered from the long-term weather station nearest to each site. Climate variables included mean October–June precipitation, July–September precipitation, maximum and minimum January temperatures, and maximum and minimum July temperatures.

Statistical Analysis

Analyses were conducted at two scales. At the "plot scale" (0.1-ha scale), each of the 100 plots was a sample unit. Nonnative species richness and cover were entered into the multiple and simple regressions as dependent variables, and other plant, soils, and topographic variables were entered as independent variables. At the "vegetation-type scale," the grand number of native and nonnative species (combined species lists from four 1000-m^2 plots in each vegetation type) and mean soil, disturbance, and topographic characteristics were used in the multiple regressions.

Simple linear regressions were used at both scales to determine the relationships of nonnative species richness and cover with native species richness and cover, topographic variables, and soil characteristics and to predict nonnative species richness and cover. Soil characteristics included percentage total nitrogen, percentage total carbon, and percentage sand, silt, and clay (percentage silt was not added into the multiple regression models to reduce multicollinearity). The forward linear multiple regression models (SYSTAT version 7.0; SPSS 1997) included only variables meeting the $P < 0.15$ criterion. Data distributions that were strongly skewed were transformed prior to analysis. Log transformations were used on the total soil N, the C:N ratio, and the number and cover of nonnative species.

We used path coefficient analysis (Dewey and Lu 1959) to evaluate the direct and indirect relationships of the environmental factors to nonnative species richness and cover. Again, we relied on forward stepwise regression, the most widely used multiple regression model (Neter and others 1990), to compare nonnative species richness and cover at multiple scales (plot scale and vegetation-type scale) in a consistent manner. This regression model may not always result in the "best" regression model for all comparisons (see Neter and others 1990, pp. 452–453), but the reported relationships agreed with field observations. Path coefficient analysis simply displays the standardized partial regression coefficient (direct influence) of an environmental factor on the dependent variable, with significant ($P < 0.05$) simple correlation coefficients (indirect influences) shown among environmental variables. The residual factors (i.e., unexplained variation) from the stepwise multiple regressions are not presented but they are easily calculated as $R_{(X)} = \%(1 - R^2)$ (Dewey and Lu 1959, Stohlgren and Bachand 1997).

Results

Mean species richness varied considerably among plots and vegetation types (Table 1), a fact underscored by the range of values recorded. Native species richness ranged from 9 species/0.1 ha in an ungrazed northern prairie type at the Charles M. Russell National Wildlife Refuge in Montana to 71 species/0.1 ha in a grazed northern prairie type at Wind Cave National Park, South Dakota. Nonnative species richness ranged from 0 species/0.1 ha in the high-elevation alpine type at Rocky Mountain National Park, Colorado, to 18 species/0.1 ha in the riparian juniper–grassland type at Bighorn Canyon National Recreation Area, Wyoming. The greatest foliar cover of nonnative species was 51%, recorded in desert grassland at Badlands National Park

Table 1. Vegetation characteristics in 100 0.1-ha plots (25 sets of 4 plots in 22 vegetation types) in the north–central United States: Mean of four to eight plots (standard error)

		Native		Nonnative	
Study area[a]	Vegetation type	Species richness	% cover	Species richness	% cover
Rocky Mountain N.P., CO	Alpine	25.0 (3.9)	74.4 (4.3)	0.0	0.0
	Aspen	50.2 (3.2)	38.7 (10.5)	5.5 (1.8)	6.4 (4.2)
	Wet meadow	35.0 (8.7)	79.0 (6.0)	6.5 (1.2)	5.8 (2.6)
	Lodgepole pine	29.0 (2.9)	8.0 (2.0)	1.5 (0.3)	0.3 (0.2)
	Dry meadow	41.5 (1.7)	44.3 (1.9)	2.0 (0.7)	0.6 (0.2)
	Ponderosa pine	34.8 (3.2)	15.6 (1.1)	2.0 (0.7)	0.2 (0.1)
	Mixed conifer	22.5 (6.1)	48.2 (15.8)	1.8 (1.2)	1.0 (1.0)
High Plains Exp. Ctr., WY	Mixed-grass prairie	35.5 (2.1)	45.9 (5.9)	2.5 (1.0)	0.04 (0.04)
Wind Cave N.P., SD	Northern mixed prairie				
	Grazed	41.6 (4.9)	31.9 (4.5)	6.8 (0.5)	20.8 (4.4)
	Riparian	56.5 (5.4)	38.1 (3.4)	9.0 (0.8)	12.0 (4.8)
Charles M. Russell N.W.R., MT	Northern mixed prairie				
	Ungrazed	23.0 (5.9)	19.8 (4.9)	1.2 (0.5)	0.4 (0.2)
	Grazed	19.4 (2.8)	19.6 (3.2)	0.8 (0.3)	0.2 (0.1)
Yellowstone/Grand Teton N.P., WY	Montane meadow				
	Ungrazed	34.0 (1.7)	56.8 (6.4)	2.5 (1.4)	0.2 (0.1)
	Grazed	34.0 (3.4)	50.0 (5.8)	3.3 (0.9)	2.0 (1.0)
Central Plains Expt. Range, CO	Short-grass upland				
	1996	26.0 (1.8)	57.5 (4.1)	1.2 (0.4)	0.04 (0.01)
	1997	29.4 (1.9)	48.2 (5.3)	1.1 (0.4)	0.03 (0.01)
	Short-grass riparian 1997	44.5 (9.6)	31.6 (5.6)	3.0 (1.1)	0.16 (0.11)
Badlands N.P., SD	Desert mixed grass upland	26.0 (2.2)	22.7 (2.0)	8.8 (1.5)	21.6 (11.4)
	Desert mixed-grass Riparian	33.0 (5.5)	37.8 (10.6)	9.5 (0.6)	2.4 (0.4)
Bighorn Canyon N.R.A., WY, MT	Mixed-grass upland	24.3 (1.7)	20.6 (2.7)	2.8 (1.9)	1.2 (1.0)
	Mixed-grass Riparian	29.0 (4.8)	38.0 (6.3)	10.0 (2.9)	20.9 (10.7)
Pipestone N.M., MN	Tallgrass prairie	37.5 (4.1)	57.6 (12.1)	8.8 (1.0)	20.4 (8.3)

[a] N.P., National Park; N.W.R., National Wildlife Refuge; N.R.A., National Recreational Area; N.M., National Monument.

in South Dakota, followed by 44% in tallgrass prairie at Pipestone National Monument, Minnesota.

Soil characteristics also varied considerably among plots and vegetation types (Table 2), again highlighted by recorded ranges. The percentage sand in the top 15 cm of soil, for example, ranged from only 2.4% in a northern prairie plot at the Charles M. Russell National Wildlife Refuge to 87.6% in a montane meadow plot in Montana (Yellowstone/Teton National Parks). Conversely the percentage clay ranged from 6.7% in an aspen plot at Rocky Mountain National Park to 89.3% at the Charles M. Russell National Wildlife Refuge. The percentage, total nitrogen in the soil ranged from 0.02% in the riparian juniper–grassland type to 0.8% in a wet meadow plot at Rocky Mountain National Park. Likewise, the percentage total carbon varied from 0.3% in the riparian juniper–grassland type to 14.2% in a mixed conifer forest plot at Rocky Mountain National Park.

There was evidence that climate and soils influenced total species richness at the 1000-m^2 plot scale. About 25% of the variation in total species richness was explained by the mean July maximum temperature, January minimum temperature, percentage clay content in the soil, October–June precipitation, and July–September precipitation ($F = 6.8$, $P < 0.001$,

Table 2. Soil characteristics in 100 0.1-ha plots (25 sets of 4 plots in 22 vegetation types) in the north–central United States: Mean of four to eight plots (standard error)

Study area[a]	Vegetation type	C (%)	N (%)	Sand (%)	Silt (%)	Clay (%)	Elevation (m)	Disturbance (class)
Rocky Mountain N.P., CO	Alpine	2.8 (0.5)	0.1 (0.02)	65.8 (1.9)	14.0 (2.3)	20.2 (0.9)	3007 (63)	1.0 (0.0)
	Aspen	3.5 (0.8)	0.1 (0.01)	75.6 (1.4)	14.3 (2.2)	10.2 (1.5)	2704 (35)	1.0 (0.0)
	Wet meadow	5.6 (1.9)	0.4 (0.2)	59.7 (11.4)	18.9 (4.4)	21.4 (7.2)	2545 (4)	1.0 (0.0)
	Lodgepole pine	4.2 (0.6)	0.2 (0.1)	72.8 (0.8)	14.5 (1.4)	12.7 (2.1)	2665 (33)	1.0 (0.0)
	Dry meadow	1.5 (0.5)	0.1 (0.03)	72.2 (1.1)	15.7 (0.5)	12.1 (1.3)	2612 (42)	1.0 (0.0)
	Ponderosa pine	3.0 (0.8)	0.1 (0.04)	77.3 (3.4)	11.8 (1.5)	10.9 (2.1)	2625 (44)	1.0 (0.0)
	Mixed conifer	7.0 (2.5)	0.3 (0.1)	66.1 (3.5)	15.8 (2.0)	18.1 (3.0)	2723 (113)	1.0 (0.0)
High Plains Expt. Ctr., WY	Mixed-grass prairie	1.8 (0.1)	0.2 (0.01)	63.0 (1.8)	11.0 (1.6)	26.0 (2.9)	1944 (13)	2.5 (1.0)
Wind Cave N.P., SD	Northern mixed prairie Grazed	3.1 (0.5)	0.3 (0.03)	23.1 (2.1)	31.9 (2.4)	45.0 (0.9)	1250 (30)	2.5 (0.5)
	Riparian	2.8 (0.1)	0.2 (0.03)	61.4 (2.9)	15.1 (2.9)	23.5 (4.4)	1187 (26)	2.5 (0.5)
Charles M. Russell N.W.R., MT	Northern mixed prairie							
	Ungrazed	1.8 (0.2)	0.2 (0.01)	17.1 (6.7)	25.8 (1.3)	57.2 (7.4)	865 (27)	2.0 (0.0)
	Grazed	1.4 (0.1)	0.2 (0.01)	19.3 (6.4)	23.1 (2.7)	57.7 (7.9)	863 (19)	3.6 (0.2)
Yellowstone/Grand Teton N.P., WY	Montane meadow							
	Ungrazed	2.7 (0.5)	0.2 (0.05)	53.7 (4.7)	25.1 (2.9)	21.2 (3.2)	2077 (63)	0.0 (0.0)
	Grazed	4.3 (0.7)	0.3 (0.06)	58.6 (4.7)	20.4 (3.5)	21.0 (2.4)	2063 (37)	2.5 (0.2)
Central Plains Expt. Range, CO	Short-grass steppe							
	Upland (1996)	0.9 (0.1)	0.1 (0.01)	74.3 (2.8)	11.1 (1.5)	14.7 (1.5)	1644 (29)	3.0 (0.4)
	Upland (1997)	0.9 (0.1)	0.1 (0.01)	72.7 (3.4)	6.1 (1.4)	21.3 (2.2)	1645 (16)	3.1 (0.2)
	Riparian (1997)	0.9 (0.2)	0.1 (0.02)	56.7 (4.2)	14.6 (1.7)	28.7 (4.8)	1620 (9)	2.3 (0.3)
Badlands N.P., SD	Desert mixed-grass							
	Upland	1.5 (0.2)	0.1 (0.01)	24.2 (5.0)	30.4 (5.2)	45.3 (8.2)	795 (27)	1.8 (0.3)
	Riparian	1.5 (0.05)	0.1 (0.02)	28.0 (8.3)	26.0 (2.5)	46.5 (8.6)	783 (16)	2.3 (0.5)
Bighorn Canyon N.R.A., WY, MT	Mixed-grass							
	Upland	2.2 (0.6)	0.1 (0.05)	53.5 (4.7)	9.9 (6.9)	36.6 (4.7)	1378 (58)	2.0 (0.0)
	Riparian	0.8 (0.2)	0.1 (0.05)	62.1 (8.6)	13.4 (6.2)	24.5 (2.7)	1161 (65)	3.5 (0.6)
Pipestone N.M., MN	Tallgrass prairie	4.4 (0.2)	0.4 (0.02)	11.7 (1.2)	54.1 (0.8)	34.3 (1.7)	498 (16)	2.8 (1.0)

[a] For abbreviations see Table 1, footnote a.

df = 5 and 86). Thus, the samples covered a very broad range of vegetation types, soils, and climatic conditions in natural areas in the north–central United States.

General Patterns of Successful Invasion

There are several general patterns of invasion at the 1000-m^2 plot scale. There were significant positive relationships between the nonnative species richness and

Table 3. Simple linear regressions of vegetation and soil characteristics as predictors of nonnative species richness and cover for the 100 1000-m^2 plots (25 sets of 4 plots in 22 vegetation types) used in the study

Dependent variable/predictors	Coefficient	t	P	Model F and r
1000-m^2 plot scale ($n = 100$ plots)				
Log No. nonnative spp.				
No. native spp.	0.013	5.08	0.001	$F = 25.8$, $r = 0.46$
Log soil % N	1.69	2.12	0.036	$F = 4.5$, $r = 0.21$
Soil (% sand + % clay)	0.003	2.00	0.048	$F = 4.0$, $r = 0.21$
Log cover nonnative spp.				
No. native spp.	0.014	3.60	0.001	$F = 13.0$, $r = 0.34$
Log No. nonnative spp.	1.12	11.9	0.001	$F = 141.8$, $r = 0.77$
Soil (% sand + % clay)	0.005	2.38	0.019	$F = 5.7$, $r = 0.24$
Log soil % N	2.92	2.60	0.011	$F = 6.8$, $r = 0.25$
Vegetation-type Scale ($n = 25$ sets of 4 plots)				
Log No. nonnative spp.				
No. native spp.	0.125	2.63	0.015	$F = 6.9$, $r = 0.48$
Soil (% sand + % clay)	0.096	1.76	0.092	$F = 3.1$, $r = 0.12$
Log cover nonnative spp.				
Log No. nonnative spp.	0.08	6.80	0.001	$F = 47.0$, $r = 0.82$
Log soil % N	4.7	1.74	0.095	$F = 3.0$, $r = 0.12$

the native species richness, total soil nitrogen, and silt + clay content in the soil (Table 3). Likewise, nonnative species cover was significantly positively correlated with those same variables at the plot scale (Table 3).

For the 100 plots throughout the study region, there was a significant negative relationship between elevation and nonnative species richness (log nonnative species richness; $r = -0.32$, $F = 11.5$, $P < 0.001$). Only the high-elevation alpine type at Rocky Mountain National Park had no nonnative species in the sample plots.

At the plot scale, 50% of the variation in nonnative species cover was explained by native plant species richness, longitude, latitude, soil total percentage nitrogen, and mean maximum July temperature (Figure 2a). For the 100 plots, 60% of the variation in nonnative species cover was explained by nonnative plant species richness, elevation, and total soil nitrogen (Figure 2b).

At the vegetation-type scale (25 sets of four plots), nonnative species richness was significantly correlated with total native species richness and total soil nitrogen (Table 3). Compared to the plot-scale results, the relationship was stronger for native species richness and weaker for soil total nitrogen. Also, at the vegetation-type scale, 64% of the variation in nonnative species richness was explained by native plant species richness, elevation, and winter (October to June) precipitation (Figure 3a). One possible interpretation is that once several nonnative species become established, a habitat may be particularly vulnerable to greatly increased cover of invasive species (Figures 3b and 4). This explanation is supported by the positive correlation between nonnative species richness and foliar cover at the plot scale ($r = 0.77$, $P < 0.001$) and vegetation-type scale ($r = 0.83$, $P < 0.001$).

Disturbance, as we classified it, showed little statistical relationship to nonnative species richness. For the 100 0.1-ha plots, the numbers of plots from low (class 0) to high (class 5) disturbance class were 5, 35, 26, 17, 15, and 2 plots. Despite this fairly broad range, there were no significant correlations between disturbance class and nonnative species richness at either the plot scale ($P = 0.56$, $F = 0.33$) or the vegetation-type scale ($P = 0.33$, $F = 0.98$).

Discussion

Reexamining the Relationship of Native Species Richness and Plant Invasion

In a previous study (Stohlgren and others 1999a) that included 9 of the 22 vegetation types used in this synthesis, we showed that nonnative species richness was strongly positively correlated with native species richness. This larger synthesis more strongly confirms that relationship at multiple spatial scales (Table 3). In both grassland and montane biomes, species-rich sites have been heavily invaded (Table 1) (Stohlgren and others 1999a). This alarming pattern may be more

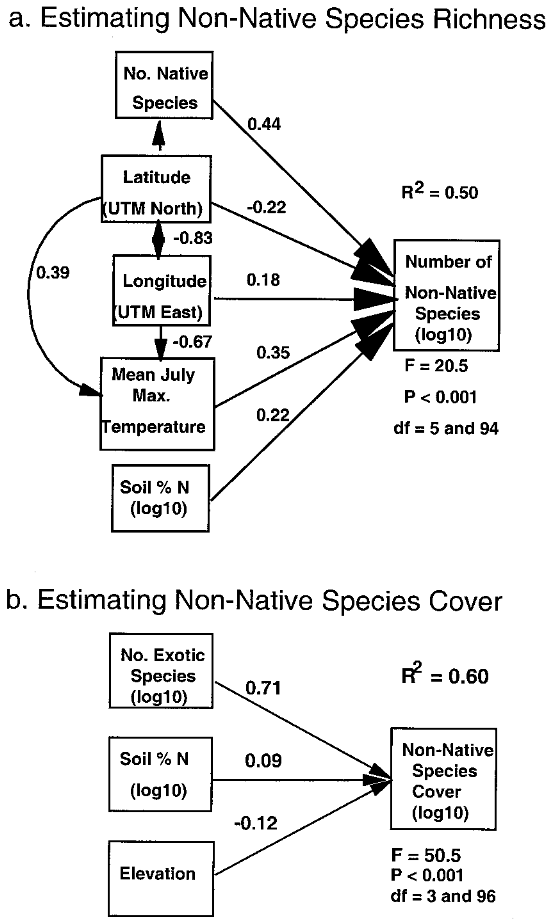

Figure 2. Path coefficient diagram of environmental factors influencing nonnative species richness (a) and cover (b) for 100 1000-m^2 plots in the north–central United States. Direct arrows to nonnative species richness or cover include standardized partial regression coefficient values, while arrows between environmental variables are simple correlation coefficients. R^2 is the adjusted coefficient of multiple determination.

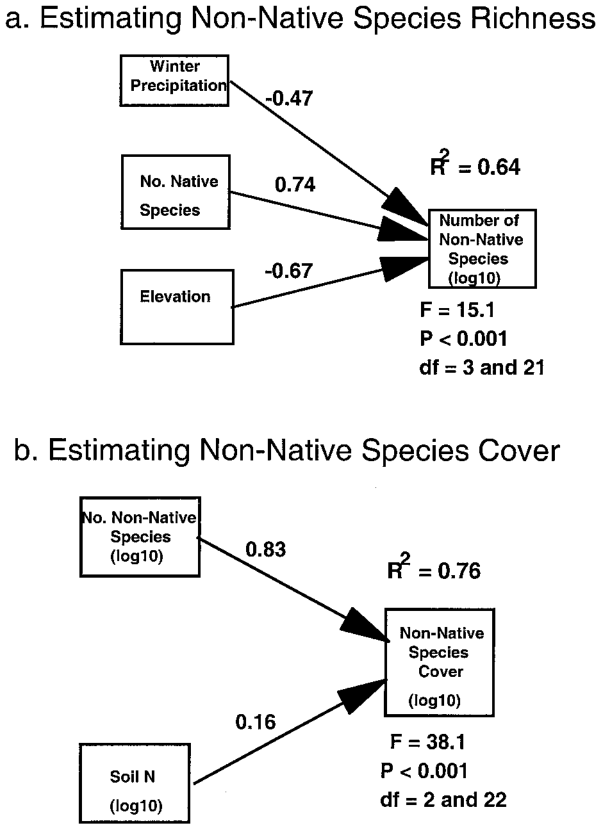

Figure 3. Path coefficient diagram of environmental factors influencing nonnative species richness (a) and cover (b) for the 25 sites (vegetation-type scale) in the north–central United States. Direct arrows to nonnative species richness or cover include standardized partial regression coefficient values, while arrows between environmental variables are simple correlation coefficients. R^2 is the adjusted coefficient of multiple determination.

widespread than previously thought. A recent landscape-scale survey in arid, southwestern Utah found similar patterns with heavy invasions in areas high in native species richness, rare habitats, and fertile soils (Stohlgren et al. 2001). In this and other landscapes, nonnative species richness was strongly positively correlated with native species richness (Table 1) (Stohlgren and others 1999a, 2000, 2001). Locally, species-rich riparian zones were more heavily invaded than species-poor upland sites nearby (Table 1) (Stohlgren and others 1998b, Planty-Tabacchi and others 1996). Of greatest concern was a stronger correlation between native and nonnative species richness at the vegetation-type scale compared to the plot scale. Species-rich vegetation types in the north–central United States appear to be highly vulnerable to invasion by nonnative species (Table 2). Conversely, there was little support for theories that areas of high species diversity might resist invasion by nonnative species (MacArthur and Wilson 1967, Turelli 1981, Post and Pimm 1983, Rummel and Roughgarden 1983, Case 1990, Law and Morton 1996). There was also little agreement with the few field studies and small-scale experiments that reported a negative relationship between native and nonnative species richness (McNaughton 1983, 1993, Fox and Fox 1986, Tilman 1997).

We do not fully understand the mechanisms and processes that create the observed patterns. Native species richness in an area is likely the result of habitat heterogeneity and available resources (Lonsdale 1999), seed supply (Coffin and Lauenroth 1989, Tilman

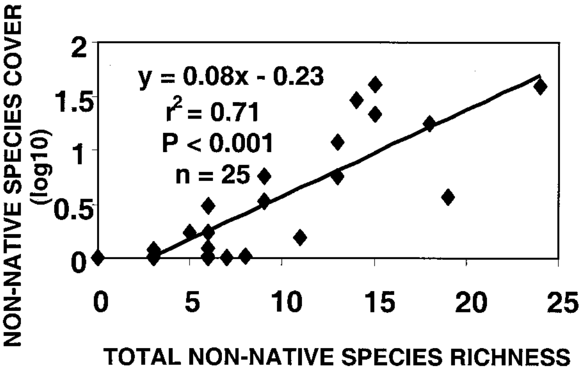

Figure 4. Relationship of total nonnative species richness at the vegetation-type scale (from sets of four 1000-m^2 plots) and mean nonnative species cover (from 40 1-m^2 subplots/vegetation type) in the north–central United States.

1997), and many other factors such as disturbance history, land use, species migration and turnover, herbivory, competition, diseases, and pathogens (Stohlgren and others 1999a). The attribute of "native species richness" may have little direct, "causal" effect on invasion potential (Rejmánek 1996a, Stohlgren and others 1999a, Lonsdale 1999, Levine and D'Antonio 1999). However, this does not diminish the importance of native species richness as an indicator or predictor of habitat vulnerability to invasion (Table 3, Figures 2 and 3). The simplest explanation may be that nonnative plant species thrive on the same resources (high light, nitrogen, and water) as native plant species (Stohlgren and others 1997a, 1998b, 1999a, 2000, 2001, Lee 2001). Information on native species richness, soil nitrogen, elevation, and precipitation are relatively easy to obtain over large areas and may greatly improve the precision and accuracy of spatial models of invasive species (Chong and others 2001).

May (1973) argued that highly diverse communities are intrinsically unstable with some species dropping in and out routinely. We observed that most species in a plot had <1% foliar cover. We also observed many species in cotyledon, seedling, and mature stages within and among plots. These small, young, individual plants and scattered subpopulations may be vulnerable to high turnover of individuals and changes in local species composition. It is easy to imagine some native species dropping out and nonnative species replacing them. Theoretically, many species can coexist as a result of biogenic small-scale heterogeneity and interactions among organisms for spatially and temporally variable resources (Huston and DeAngelis 1994), but species replacements also may occur in areas of high turnover (Stohlgren and others 1999a,b, 2000a).

It appears that landscape-scale and biome-scale study results are ignored or discounted by those claiming that species-rich areas are more stable and less-invasible than species-poor areas (e.g., Tilman 1997, 1999, Mack and others 2000). A growing number of landscape-scale (DeFerrari and Naiman 1994, Stohlgren and others 1997a, 1999c, 2000, 2001, Lee 2001), biome-scale (Stohlgren and others 1999a), regional-scale (this study), and global-scale (Vitousek and others 1996, Rejmánek 1996, Lonsdale 1999) studies clearly show that many species-rich areas in the world have been readily invaded by nonnative plant species.

There are many other possible causes for the patterns of invasion reported in this paper. Propagule pressure by nonnative species may be disproportionately higher in certain areas, but it is difficult and impractical to measure, monitor, regulate, or manage propagule pressure at landscape scales, especially for seeds that are ubiquitously distributed by wind, large and small mammals, and insects (Stohlgren and others 2001). The origin, autecology, and genetic variation of the nonnative invaders may also be important (Mack and others 2000). That is, the nonnative species pool may include species that favor fertile sites. However, the traits of herbaceous plant species have not proven to be of general predictive value for invasions at landscape scales. Lee (2001) showed that plant species traits explained only about 12% of the variation in invasion success, while habitat characteristics explained 60% of the invasion success in Rocky Mountain National Park, Colorado. Escape from natural enemies may add to the success of nonnative species (Mack and others 2000), but this is very difficult to quantify over landscape and regional scales for many species.

Habitat characteristics are unquestionably important predictors of successful invasions (Table 3, Figures 2 and 3), and they are relatively easier and inexpensive to measure and monitor (Stohlgren and others 1998b, 1999a, 2001). Isolating the causes of the patterns reported here are beyond the scope of this observational study. Instead, we draw the land manager's attention to the locations, habitats, and physical factors associated with the current patterns of successful invasion to aid in future control and restoration efforts (Stohlgren and others 2001).

Reexamining the Effects of Grazing and Disturbance on Plant Invasions

In most of our study sites, disturbances such as grazing by ungulates and domestic animals had minimal effects on nonnative species richness. Intensive grazing by cattle for over 100 years at the relatively species-poor short grass steppe of Colorado has resulted in little invasion by nonnative species (Stohlgren and others 1999a). There were no significant differences in native and nonnative species richness and cover between long-term grazed and ungrazed plots at the Charles M. Russell National Wildlife Refuge or in Yellowstone/Teton National Parks (Table 1) (Stohlgren and others 1999b). Nonnative species appear to be invading and thriving in both grazed and long-term ungrazed sites in our study areas (Stohlgren and others 1999b). These sites tended to have long evolutionary histories of grazing (Milchunas and Lauenroth 1993).

Disturbance, as we classified it, had little effect on native and nonnative species richness in the sites we studied. It may be that superficial disturbances, such as removal of aboveground biomass by herbivores, are less devastating than a plow, a road grader, or excavations by small mammals which churn the soil. Traveling to our study sites, we observed invasive plants along nearly all of the roadways and edges of agricultural lands. Although we detected no invasive plants at high-elevation alpine sites at Rocky Mountain National Park, Colorado, probably because most Mediterranean weeds in the area cannot tolerate cold temperatures (Stohlgren and others 2000b), the common dandelion (*Taraxacum officinale*) can be found along high elevation road cuts and trails.

The potential role of other disturbances such as large-scale fire, small ground-churning mammals, insect and disease outbreaks, and flooding was not assessed in this study, and they deserve more attention in future research (Hobbs and Hueneke 1992). Likewise, activities that increase available nitrogen on a site (e.g., fire, air pollution, fertilization, nitrogen-fixing plants) may promote invasion, especially if the site is near and connected to an already infested site.

Management Implications

Land managers may not be able to seek solace in the prevailing paradigm (and hope) that establishment by nonnative species in natural landscapes should decline in the face of many strongly interacting native species, which are thought to use resources more completely. Although the mechanisms are far from clear, we found patterns of invasion that produce significant challenges for land managers. Habitats with high native species richness were more heavily invaded than species-poor habitats as evidenced by strongly significant correlations between native and nonnative species at the plot scale and across vegetation types. Control and restoration activities will have to be carefully planned and executed in many habitats. There should be reluctance to broadcast herbicides in hotspots of native plant diversity. More efficient and selective biological control efforts are needed. Far more research is needed on the effects of nonnative species in native species-rich habitats. For example, the best predictors of native butterfly richness at Rocky Mountain National Park, Colorado were the richness and cover of nonnative plant species (Simonson and others 2001). Additional research is needed to determine the long-term ramifications of the establishment and spread of nonnative plants into hotspots of native biodiversity.

Low-elevation areas were more heavily invaded than high-elevation sites, and species-rich riparian zones tended to have more nonnative species than adjacent upland sites. Land managers in mountainous areas may have to contend with an increasing pressure of invasions from lowland areas and riparian zones that may serve as corridors of invasion. The spatial matrix of roadside disturbance and riparian zones may provide continuous sources of seeds to riparian and adjacent upland sites.

Canopy gaps in forests, aspen stands, and productive montane meadows were more heavily invaded than closed-canopy forests with sparse understory vegetation (Table 1) (Stohlgren and others 2000, Lee 2001). Land managers may be in the awkward position of protecting forests, while allowing for resource extraction or natural fire regimes, which may promote nonnative plant invasions.

Grazed and ungrazed sites and disturbed and undisturbed sites are all vulnerable to invasion as long as light, water, and nitrogen are available (Table 1) (Stohlgren and others 1999b). While disturbance may enhance invasion in some of these habitats, the subtle invasion in less disturbed sites may be particularly difficult to manage for and control over large areas.

Nonnative plant invasions in rare habitats and distinctive plant communities pose the most significant challenge to land managers and conservation biologists charged with protecting native biodiversity. Tallgrass prairie, riparian zones, aspen stands, and wet meadows often contain unique assemblages of plant species—and these habitats appear to be particularly vulnerable to invasion. Early detection of nonnative species, and control and restoration efforts may be more difficult in species-rich environments. More sophisticated and extensive inventory and monitoring programs are needed. Many agencies, states, and nongovernment organizations have begun extensive control and restoration efforts, without commensurate research and monitoring efforts to assess environmental costs to native species in the area. Managers need far better spatial and ecosystem models to predict the establishment and spread of invasive plant species (Chong and others 2001).

Acknowledgments

Helen Fields, April Owen, and Elizabeth Smith assisted with the fieldwork in the Colorado Rockies. Debbie Casdorph, Randy Griffis, Stephanie Neeley, and Mary Damm assisted with the fieldwork in the Central Grasslands. The U.S. Geological Survey provided funding for the research. We received strong logistical support from the staffs of Rocky Mountain National Park, the Natural Resource Ecology Laboratory at Colorado State University, and the Midcontinent Ecological Science Center (U.S. Geological Survey). Dan Reuss and James Self provided extensive soils analysis help. Ross Rice, Mark Lindquist, Dick Hart, Todd Suess, and Dave Kenny also provided logistical support. James O. Luken, Shawn Smallwood, and Diana E. Marco provided many helpful suggestions to the manuscript. To all we are grateful.

Literature Cited

Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invisibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution, and Systematics* 3:52–66.

Carter, M. R. (ed.) 1993. Soil sampling and methods of analysis. Lewis, Boca Raton, FL, 387 pp.

Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Science USA* 87:9610–9614.

Chong, G. W., R. M. Reich, M. A. Kalkhan, and T. J. Stohlgren. 2001. New approaches for sampling and modeling native and exotic plant species richness. *Western North American Naturalist* 61:328–336.

Coffin, D. P., and W. K. Lauenroth. 1989. The spatial and temporal variability in the seed bank of a semiarid grassland. *American Journal of Botany* 76:53–58.

Crawley, M. J. 1987. What makes a community invasible? Pages 429–453 *in* A. J. Gray, M. J. Crawley, and P. J. Edwards (eds.) Colonization, succession, and stability. Blackwell Press, Oxford.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.

Darwin, C. 1859. The origin of species. Reprinted by Penguin Books, London, 237 pp.

DeFerrari, C. M., and R. J. Naiman. 1994. A multi-scale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. *Journal of Vegetation Science* 5:247–258.

Dewey, D. R., and K. H. Lu. 1959. A correlation and path-coefficient analysis of components of crested wheatgrass seed production. *Agronomy Journal* 51:515–518.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London, 259 pp.

Fox, M. D., and B. J. Fox. 1986. The susceptibility of natural communities to invasion. Pages 57–60 *in* R. H. Groves and J. J. Burdon (eds.) Ecology of biological invasions. Cambridge University Press, Cambridge.

Gee, G. W., and J. W. Bauder. 1986. Particle size analysis. Pages 383–411 *in A. Klute (ed.)* Methods of soil analysis. Part 1. Physical and mineralogical methods, 2nd ed., ASA, Madison, WI.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology* 6:324–337.

Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: The effects of resource transport and supply rates. *American Naturalist* 144:954–977.

Law, R., and R. D. Morton. 1996. Permanence and the assembly of ecological communities. *Ecology* 77:762–775.

Lee, M. 2001. Non-native plant invasions in Rocky Mountain National Park: Linking species traits and habitat characteristics. Masters thesis. Graduate Degree Program in Ecology, Colorado State University, Fort Collins.

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

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: A review of evidence linking diversity and invasibility. *Oikos* 87:15–26.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536.

Loope, L. L., and D. Mueller-Dombois. 1989. Characteristics of invaded islands, with special reference to Hawaii. Pages 257–280 *in* J. A. Drake, F. DiCasti, R. H. Groves, F. J. Kruger, H. A. Mooney, M. Rejmánek, and M. H. Williams (eds.) Biological invasions: A global perspective. John Wiley and Sons, New York.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ, 201 pp.

Mack, R. N., D. Simberloff, W. M Lonsdale, H. Evans, M. Clout, and F. Bazzaz. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Society of America, Issues in Ecology* 5, 20 pp.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, NJ, 238 pp.

McNaughton, S. J. 1983. Serengeti grassland ecology: The role of composite environmental factors and contingency in community organization. *Ecological Monographs* 53:291–320.

McNaughton, S. J. 1993. Biodiversity and function of grazing ecosystems. Pages 361–383 *in* E. D. Schulze and H. A. Mooney (eds.) Biodiversity and ecosystem function. Springer-Verlag, Berlin.

Milchunas, D. G., and W. K. Lauenroth. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63:327–366.

Moulton, M. P., and S. L. Pimm. 1986. Species introductions to Hawaii. Pages 231–249 *in* H. A. Mooney and J. A. Drake (eds.) Ecology of biological invasions of North America and Hawaii, Springer-Verlag, New York.

Neter, J., W. Wasserman, and M. H. Kutner. 1990. Applied linear statistical models: Regression, analysis of variance, and experimental designs, 3rd ed. Irwin, Homewood, IL, 498 pp.

Planty-Tabacchi, A., E. Tabacchi, R. J. Naiman, C. DeFerrari, and H. Décamps. 1996. Invasibility of species-rich communities in riparian zones. *Conservation Biology* 10:598–607.

Post, W. M., and S. L. Pimm. 1983. Community assembly and food web stability. *Mathematical Bioscience* 64:169–192.

Rejmánek, M. 1996. Species richness and resistance to invasions. Pages 153–172 *in* H. Orians, R. Dirzo, and J. H. Cushman (eds.) Biodiversity and ecosystem processes in tropical forests, Ecological Studies, Vol. 122, Springer-Verlag, Berlin.

Robinson, G. R., and J. F. Quinn. 1988. Extinction, turnover and species diversity in an experimentally fragmented California annual grassland. *Oecologia* 76:71–82.

Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat in California winter annual grassland. *Ecology* 76:786–794.

Rummel, D. J., and J. Roughgarden. 1983. Some differences between invasion-structured and coevolutionary-structured competitive communities. *Oikos* 41:477–486.

Simonson, S. E., P. A. Opler, T. J. Stohlgren, and G. W. Chong. 2001. Rapid assessment of butterfly diversity in a montane landscape. *Biodiversity and Conservation* 10:1369–1386.

Smallwood, K. S. 1994. Site invasibility by exotic birds and mammals. *Biological Conservation* 69:251–259.

Stohlgren, T. J., and R. R. Bachand. 1997. Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. *Ecology* 78:623–641.

Stohlgren, T. J., M. B. Falkner, and L. D. Schell. 1995. A modified-Whittaker nested vegetation sampling method. *Vegetation* 117:113–121.

Stohlgren, T. J., G. W. Chong, M. A. Kalkhan, and L. D. Schell. 1997. Rapid assessment of plant diversity patterns: A methodology for landscapes. *Environmental Monitoring and Assessment* 48:25–43.

Stohlgren, T. J., K. A. Bull, and Y. Otsuki. 1998a. Comparison of rangeland sampling techniques in the Central Grasslands. *Journal of Range Management* 51:164–172.

Stohlgren, T. J., K. A. Bull, Y. Otsuki, C. Villa, and M. Lee. 1998b. Riparian zones as havens for exotic plant species. *Plant Ecology* 138:13–125.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999a. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69:25–46.

Stohlgren, T. J., L. D. Schell, and B. Vanden Heuvel. 1999b. Effects of grazing and soil characteristics on native and exotic plant species in Rocky Mountain grasslands. *Ecological Applications* 9:45–64.

Stohlgren, T. J., A. J. Owen, and M. Lee. 2000. Monitoring shifts in plant diversity in response to climate change: A method for landscapes. *Biodiversity and Conservation* 9:65–86.

Stohlgren, T. J., Y. Otsuki, C. Villa, M. Lee, and J. Blenap. 2001. Patterns of plant invasions: a case example in native species hotspots and rare habitats. *Biological Invasions* 3:37–50.

Tilman, D. 1982. Resource competition and community structure, Monographs in Population Biology. Princeton University Press, Princeton, NJ, 211 pp.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81–92.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80: 1455–1475.

Timmins, S. M., and P. A. Williams. 1991. Weed numbers in New Zealand's forest and scrub reserves. *New Zealand Journal of Ecology* 15:153–162.

Turelli, M. 1981. Niche overlap and invasion of competitors in random environments. Models without demographic stochasticity. *Theoretical Population Biology* 20:1–56.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: Towards an integration of population biology and ecosystem studies. *Oikos* 57:7–13.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:468–478.

Westbrooks, R. 1998. Invasive plants, changing the landscape of America: Fact book. Federal Interagency Committee for the Management of Noxious and Exotic Weeds (FICMNEW), Washington, DC, 109 pp.