

# Patch dynamics of a native grass in relation to the spread of invasive smooth brome (*Bromus inermis*)

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**Abstract** The effects of invasive species on the patch dynamics (establishment, growth, and local extinction) of native species are not well studied, owing to the need for relatively fine-scale data on the distribution of species. Within the prairie pothole region of the United States and Canada, the grass, *Bromus inermis* (smooth brome) has become established by invading disturbed prairies, and through repeated introductions for soil retention and animal graze. In this study, the impact of smooth brome on the patch dynamics of a dominant native grass species, *Spartina pectinata* (prairie cordgrass), was assessed using fine-scale (sub-meter) mapping of the distribution of cordgrass and brome in three prairie fragments from 2000 to 2006. Using GIS spatial analyses, we determined that cordgrass patch growth was two times greater in areas not invaded by smooth brome versus areas that were heavily infested with smooth brome. Among sites and time periods, there was a consistent significant negative relationship between the amount of smooth brome surrounding a patch of cordgrass and the growth of that cordgrass patch. The probability of establishment of a new patch of cordgrass averaged 1.3 times higher in areas of low brome coverage (<25%) than areas of high brome coverage (>75%).

Conversely, existing cordgrass patches were 7.8 times more likely to go extinct in areas of high than low brome coverage. This is one of only a few field studies to provide evidence of the negative impact of smooth brome on native flora and hopefully will serve as justification for the development of a formal management plan to limit the distribution of this species in tallgrass prairie ecosystems.

**Keywords** *Bromus inermis* · *Spartina pectinata* · Invasive species · Geographical information systems (GIS) · Colonization · Establishment · Extinction · Patch dynamics

## Introduction

Over the past 200 years, the number of non-native species within a community has increased precipitously due to human migration and commerce (Hodkinson and Thompson 1997; Kowarik 2003; Mack et al. 2000; Mooney et al. 1986; Vitousek 1997). Invasive plants pose significant threats to native communities by altering ecosystems processes (Bart and Hartman 2000; Dyer and Rice 1999; Ehrenfeld 2003; Mack et al. 2001; Vitousek and Walker 1989), biodiversity levels (Brown and Gurevitch 2004) and community structure (Garci'a-Robledo and Murcia 2005; Gratton and Denno 2005). Moreover, invasive species are considered one of the top two factors (along with habitat loss/fragmentation)

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influencing extinction risk of native species (Clavero and Garcia-Berthou 2005; Wilcove et al. 1998). To understand the invasion process and the impact that invasive species have on native species, it is of paramount importance to develop programs that monitor the spread of invasive species and the associated changes in the distributional patterns of native species over time (Stohlgren et al. 1998; Thomson 2005).

Classic reaction–diffusion theory predicts the smooth and gradual spread of invasive organisms into novel habitats (Fisher 1937; Skellam 1951), and large, regional-scale distributional studies tend to support this notion (reviewed in Hengeveld 1989). However, when examined at finer spatial scales (e.g., within a forest stand or grassland fragment), invaded habitats are often heterogeneous and characterized by a mosaic of small and isolated local populations (or patches) of the invasive and native species (for example, see Johnson et al. 2006). At this smaller scale, the spatial and temporal distribution of patches of native and invasive species may be quite dynamic (Chabrierie et al. 2007) and the complete displacement of native species may never occur (Sax et al. 2002). It is at this scale that native–invasive interactions take place (Gurevitch et al. 2002; Theoharides and Dukes 2007). Fine-scale (sub-meter) monitoring programs may be necessary for the detection of the effects of invasive species on the patch dynamics (growth, local extinction and establishment) of native species (e.g., Barbraud et al. 2003; Bradley and Mustard 2006; Lass et al. 2005).

Remote sensing has become a popular and valuable tool for monitoring the spread of invasive plant species, and associated changes in the distribution of native flora (Pengra et al. 2007). The advantages of remote sensing are well known and include the collection of data that span broad spatial and temporal scales. However, the usefulness of remote sensing is limited by the accessibility of data for certain regions, coarse resolution of data (e.g., 30 m<sup>2</sup> pixel size with Landsat Thematic Mapper data; Madden 2004; Mladinich et al. 2006), and prohibitive costs associated with multi or hyperspectral data that are necessary to differentiate plant species.

Ground-based approaches that use traditional surveying equipment or global positioning systems (GPS) are time consuming and labor intensive (Everitt et al. 1992), but have distinct advantages over remote

sensing. Most notably, ground surveys can resolve fine-scale distributional patterns of species (<1 m)—the scale at which species interactions are likely to be strongest (e.g., interspecific competition; Gurevitch et al. 2002). Moreover, structurally or spectrally similar species may be indistinguishable with available remote sensing data and can only be separated by competent botanists in the field. Finally, the patterns of establishment and extinction of native and invasive plant patches can be discerned with traditional ground surveys. For example, by mapping and monitoring the spread of the invasive perennial herb, *Hieracium lepidulum*, Wiser et al. (1998) were able to determine that the invasion patterns were related to dispersal limitation, community structure, disturbance history, and environmental characteristics.

In this study, we employ a fine scale (sub-meter) GPS survey spanning 6 years to quantify the change in distributional patterns of invasive smooth brome (*Bromus inermis* Leyss) and a dominant native grass (prairie cordgrass, *Spartina pectinata* Link) within tall-grass prairie fragments of eastern North Dakota. Currently, no information is available on the spread of smooth brome at large or small spatial scales, or on how temporal changes in the distribution of smooth brome affect the distribution of native plant species. Our survey involved mapping the distribution of all clonal patches of brome and cordgrass in three prairie fragments from 2000 to 2006. Specific objectives of this survey included determining (1) the change in habitat coverage of prairie cordgrass over time, (2) whether the growth of cordgrass patches were correlated with the proportion of smooth brome adjacent to those patches, and (3) whether the extinction of existing cordgrass patches or establishment of new cordgrass patches was related to the prevalence of brome in the surrounding area.

## Methods

### Invasive smooth brome

In North America, the vast majority of native prairie habitat has been converted into agricultural land (Stoner and Joern 2004). Consequently, prairies are one of the most imperiled ecosystems in the world (Stoner and Joern 2004). To date, native mixed prairie habitat has been reduced by approximately

70% (Samson et al. 2004) with the remaining prairie fragments supporting up to 50 invasive species, roughly 12.5% of all plant species present (North Dakota Department of Agriculture 2007), many of which were intentionally introduced into the region for agricultural purposes (Mack et al. 2000; Seabloom et al. 2006; Weston and Duke 2003).

Smooth brome was originally introduced into North America in the late 1880s from Hungary and Russia (Hitchcock 1963) for soil retention and to provide animal graze (Larson et al. 2001). More recently, brome has escaped from its planted habitats and become established in native remnant prairies (D'Antonio and Vitousek 1992). At present, smooth brome has received little attention as an invasive species (but see Blankespoor and Larson 1994), despite the fact that its invasive status has been often noted (Cronin 2007; Cronin and Haynes 2004; Haynes and Cronin 2003; Otfinowski et al. 2007; Williams and Crone 2006). For instance, Williams and Crone (2006) developed a demographic model based on natural patches that indicated smooth brome is capable of slowing the growth and promoting the extinction of native *Anemone patens* (Pasque flower) patches. Similarly, in a greenhouse study, brome has been shown to maintain a high competitive ability under a variety of abiotic conditions (Nernberg and Dale 1997). At the community level, smooth brome can alter native plant diversity and increase homogenization of native habitats (Otfinowski et al. 2007). Finally, several authors have demonstrated that brome significantly impacts the movement behavior and population dynamics of several native arthropod species (Baum et al. 2004; Cronin 2003a, b, 2007; Cronin and Haynes 2004; Cronin et al. 2004; Haynes and Cronin 2003). For example, smooth brome promotes high rates of dispersal of a planthopper (*Prokelisia crocea*) and its parasitoid (*Anagrus columbi*) among patches of prairie cordgrass, and this results in local and regional extinction of their populations (Cronin and Haynes 2004; Cronin 2007).

### Study system

Our study was conducted in Kellys Slough National Wildlife Refuge in Grand Forks County, North Dakota (47.941848 N, 97.310368 W). Kelly's Slough was developed to establish and manage wetlands and grasslands unique to the Red River Valley (USFWS

2008). Within this refuge, there are approximately 355 ha of protected habitat with the upland areas comprised primarily of grasslands. A dominant native grass species in these prairie fragments is prairie cordgrass (Hitchcock 1963). Cordgrass grows clonally and forms discrete patches that range in size from a few stems to over 4 ha (Cronin 2003a). Most other native grass species grow in very diffuse patterns with no clear dominant species present. These species include foxtail barley *Hordeum jubatum* L., western wheatgrass *Agropyron smithii* Rydb., and little blue-stem *Andropogon scoparius* Michx. These prairie fragments also contain mudflats, which are slightly lower in elevation and mostly consist of bare ground and saltwort (*Salicornia rubra* Nels.) in dry periods and are covered by water in wet periods.

Smooth brome was likely introduced into Kellys Slough around the early to mid 1900s (K. Tompkins, Refuge Manager, Kellys Slough National Wildlife Refuge, personal communication) and to date, expansive monocultures of smooth brome occupy the prairie (Cronin 2003a; Haynes and Cronin 2003). Currently, the United States Fish and Wildlife Service employs a broad spectrum management plan within the Kellys Slough refuge system to reduce abundances of a variety of woody and invasive species (Emery and Gross 2005; Simmons et al. 2007; K. Tompkins, personal communication). Management involves a combination of prescribed burns, tillage, haying, grazing, and chemical treatments.

### Vegetation mapping

The position and perimeters of all cordgrass patches ( $\geq 0.25$  m<sup>2</sup>) were mapped in three different field sites within the Kelly's Slough drainage system (Site 104, Limehouse, and North Kelly's). Field sites ranged in size from 36 to 55 ha (Table 1). Mapping was conducted at three different time periods (June of 2000 and 2004 and July of 2006) using either a Leica Geosystems 500 (with Coast Guard beacon receiver) or a Trimble GeoXT (WAAS enabled) system. Both systems had a  $< 3/4$  m<sup>2</sup> margin of error. For patches of cordgrass to be considered distinct from one another, they had to be separated  $> 0.5$  m (Cronin 2003a, b, c). Smooth brome was only mapped in the latter two census periods. For both plant species, we used a GPS unit set to record positions at 1-s intervals, and walked the perimeter of every patch within a site. For

**Table 1** Summary statistics for the three field sites, Site 104, Limehouse, and North Kelly

Prairie fragment	Area (ha)	2000			2004			2006		
		Cordgrass coverage (%)	Cordgrass patches (N)	Cordgrass coverage (%)	Brome coverage (%)	Cordgrass patches (N)	Cordgrass coverage (%)	Brome coverage (%)	Cordgrass patches (N)	
Site 104	46	17	704	12	10	282	16	12	647	
Limehouse	36	19	274	18	27	162	19	30	280	
North Kelly	33	27	340	24	27	139	25	26	228	
Mean $\pm$ 2 SE	45.7 $\pm$ 2.06	21 $\pm$ 1.53	439 $\pm$ 10.14	18 $\pm$ 1.63	21.3 $\pm$ 2.09	194.3 $\pm$ 5.84	20 $\pm$ 1.43	22.7 $\pm$ 2.05	385 $\pm$ 10.07	

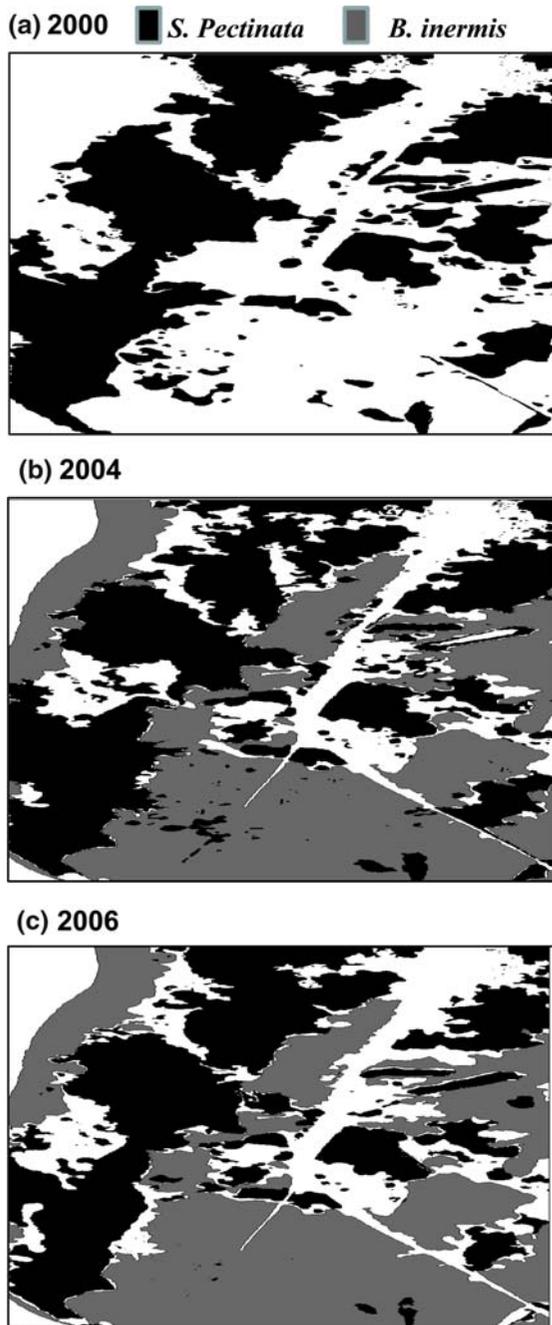
Data are divided among three time periods (2000, 2004, and 2006)

each cordgrass patch in 2004 and 2006, we also quantified the proportion of the habitat within a 1-m buffer area that was composed of brome. These data were used to determine if the amount of neighboring brome was correlated with the growth rates of cordgrass patches. We chose a distance of 1 m because smooth brome and prairie cordgrass are capable of spreading by this distance during a single growing season (Otfinowski et al. 2007; USDA and NRCS 2008). Therefore, competitive interactions are likely to take place within this buffer area. We used the following proportional categories to characterize the amount of brome within this buffer area: (1) <25%, (2) 25–50%, (3) 50–75%, and (4) 75–100%.

We imported prairie cordgrass and smooth brome positional data into ESRI® ArcMap™ 9.0. A separate database was created for each field site, and each plant species—year combination was treated as a separate theme (or layer) (Fig. 1). Patches that broadly overlapped between years were considered to be the same patch. We used the ArcMap Extension, XTools Pro v. 2.2 (Delaune and Chikinev 2005), to calculate the area of each field site and each patch of smooth brome and cordgrass. To calculate the percent coverage of each plant species within a field site, we summed patch areas and then divided this sum by the total area of the site.

Temporal trends in patch size were evaluated with a repeated-measures ANOVA. Site was a fixed factor and patch size at different census periods was the repeated measure. The purpose of the test was to assess whether changes in mean patch size over time differed among the three prairie sites (a significant time  $\times$  site interaction). Following a significant time effect, differences between any two time periods were assessed with separate paired *t*-tests. To guard against inflated type I errors associated with three different tests, a sequential Bonferroni correction was used to assess significance.

To determine how the establishment of brome influenced the growth of cordgrass patches, we computed the annual rate of change in area for each patch *i* for the time periods 2000–2004, 2004–2006, and 2000–2006. Here, the annual rate of change in size of patch *i* equals  $A_{i+1}/A_i$  divided by the number of years between surveys. *A* is patch area in m<sup>2</sup>. This growth rate scales from zero (e.g., patch extinction) to infinity. No growth rate was computed for patches that were absent at the start of the time period. The



**Fig. 1** The spatial distribution of cordgrass and brome patches in a portion of the field site North Kellys (a) cordgrass patches in 2000, (b) cordgrass and brome in 2004, and (c) cordgrass and brome in 2006. Brome distribution was not mapped in 2000 and is therefore unknown

distribution of growth rates was strongly right-skewed. Therefore, we employed a non-parametric Kruskal–Wallis test to determine whether cordgrass growth rate

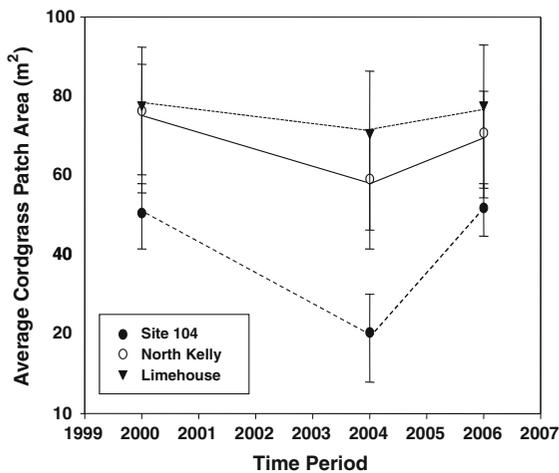
(dependent variable) was related to the percent brome (<25%, 25–50%, 50–75%, and 75–100%) adjacent to the patch (independent variable). A sequential Bonferroni correction was used to adjust for potentially inflated type I errors associated with multiple non-independent tests (i.e., the three time periods within a site). Differences between categories of brome were assessed with non-parametric Mann–Whitney *U* tests.

#### Establishment and extinction of cordgrass patches

We tested the hypothesis that the establishment of new cordgrass patches and the extinction of existing patches between time periods were significantly related to the proportional coverage of brome immediately surrounding the patch. We determined the number of cordgrass patches per brome-coverage category that remained extant between time periods (e.g., patch that was present in 2000 and 2006), were newly established (e.g., patch not present in 2000 but present in 2006) and went extinct (e.g., patches present in 2000 but not 2006). Separate chi-square tests for independence were performed to determine if cordgrass establishment and extinction likelihood differed significantly between areas differing in brome coverage. Data from all three-field sites were combined into patches that had <50% or >50% brome surrounding a patch of cordgrass. This procedure ensured that sample sizes per brome and extinction/establishment categories were sufficient to perform the chi-square tests ( $n > 5$  per category). We predicted that cordgrass extinctions would be more common and establishments would be less common in brome-dominated areas. Because extinction rates were expected to be greater for small, as compared to large, cordgrass patches, we also tested whether cordgrass patch size was confounded with brome coverage. Differences in patch size between areas of high and low brome coverage were evaluated with a paired *t*-test for each time period. We used a  $\ln$  transformation on patch area for each period in order to meet assumptions of normality.

#### Results

Mean patch size varied among years ( $F = 8.482$ ,  $df = 2$ , and  $P < 0.001$ ) (Fig. 2) and did not vary across sites ( $F = 1.016$ ,  $df = 2$ , and  $P > 0.36$ ).



**Fig. 2** The mean  $\pm$  SE cordgrass patch size ( $\text{m}^2$ ) for each time period measured. Separate symbols were used for each field site

There was no significant time  $\times$  site interaction ( $F = 2.360$ ,  $df = 4$ , and  $P > 0.05$ ). From 2000 to 2004, mean cordgrass patch size declined by an average of 16% ( $-27.4 \text{ m}^2 \pm 14.701$ ,  $P$ -value  $< 0.001$ ) across all three field sites, whereas from 2004 to 2006, cordgrass patches significantly increased in size by 12% ( $19.577 \text{ m}^2 \pm 8.5276$ ,  $P$ -value  $< 0.001$ ). As a consequence, there was no significant net change in cordgrass patch size over the 6 years of this study ( $P$ -value  $> 0.791$ ) (Fig. 2).

The growth rate of cordgrass patches was significantly affected by the proportion of smooth brome adjacent to the patch in all but one of the nine possible tests (three sites and times three time periods; Table 2). In general, growth rates declined as the proportion of brome increased (Fig. 3). For example, from 2000 to 2006, cordgrass patch growth was approximately two times greater for patches with  $<25\%$  versus patches with  $75\text{--}100\%$  brome surrounding the patch ( $\chi^2 = 24.93$ ,  $df = 2$ , and  $P < 0.001$ ).

New cordgrass patches were 1.5 (2000–2004:  $\chi^2 = 16.253$ ,  $P < 0.001$ ), 1.2 (2004–2006:  $\chi^2 = 4.975$ ,  $P < 0.036$ ), and 1.3 (2000–2006:  $\chi^2 = 5.43$ ,  $P < 0.020$ ) times more likely to become established in areas consisting of  $<50\%$  brome than areas of  $\geq 50\%$  brome (Fig. 4). Similarly, cordgrass patch extinctions were very strongly affected by brome coverage. Extinction of cordgrass patches was 1.4 (2000–2004;  $\chi^2 = 13.487$ ,  $P > 0.001$ ), 2.3 (2004–2006;  $\chi^2 = 37.542$ ,  $P < 0.001$ ), and 7.8 (2000–2006;

**Table 2** Results from separate Kruskal–Wallis tests for the effect of percent brome surrounding a cordgrass patch ( $<25\%$ ,  $25\text{--}50\%$ ,  $50\text{--}75\%$ , and  $>75\%$ ) on the percent change in cordgrass area

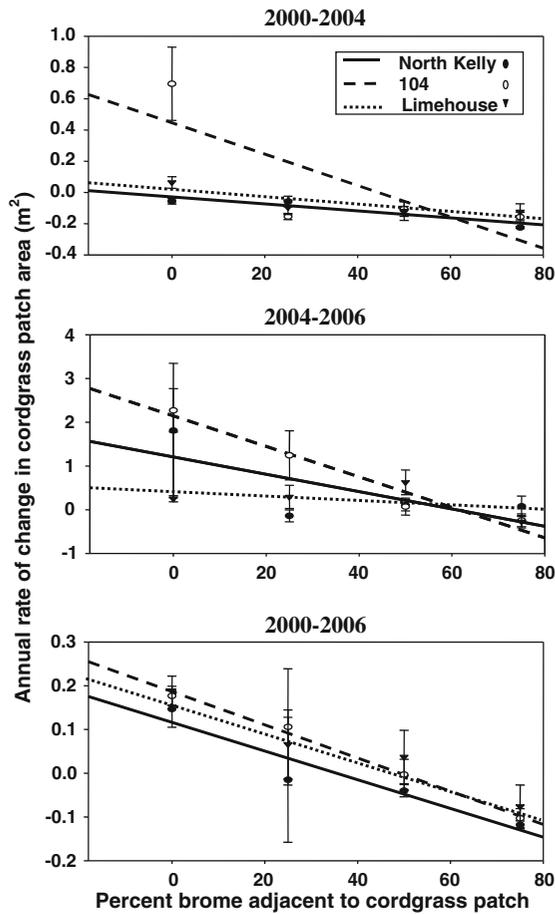
Site	Year	df	$\chi^2$	Bonferroni $P$ -value
North Kelly	2000–2004	4	100.007	$<0.001$
	2004–2006	4	13.788	$<0.027$
	2000–2006	4	85.153	$<0.001$
Site 104	2000–2004	4	21.601	$<0.001$
	2004–2006	4	60.595	$<0.001$
	2000–2006	4	135.095	$<0.001$
Limehouse	2000–2004	4	16.183	$<0.009$
	2004–2006	4	11.260	$<0.090$
	2000–2006	4	29.150	$<0.047$

Bonferroni-adjusted  $P$ -values are reported and account for potentially inflated type I errors associated with multiple tests per field site

$\chi^2 = 237.92$ ,  $P < 0.001$ ) times more likely in areas  $\geq 50\%$  relative to areas  $<50\%$  brome coverage (Fig. 4). The cause for the relatively high extinction risk of cordgrass patches in brome-dominated areas is not a consequence of smaller cordgrass patches being associated with high areas of brome. In fact, we found the opposite pattern. Mean cordgrass patch size was greater in areas of high versus low brome for every time period (mean difference in 2000 =  $1.494 \text{ m}^2$ ,  $df = 167$ ,  $t = 10.123$ ,  $P < 0.001$ ; mean difference in 2004 =  $0.862 \text{ m}^2$ ,  $df = 95$ ,  $t = 2.343$ ,  $P < 0.001$ ; and mean difference in 2006 =  $1.243 \text{ m}^2$ ,  $df = 95$ ,  $t = 4.11$ ,  $P < 0.001$ ).

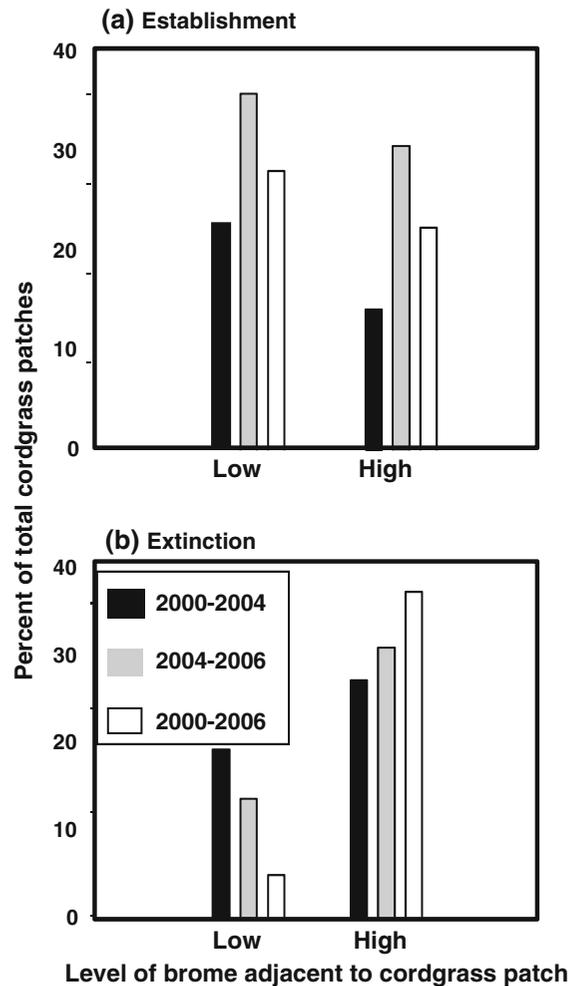
## Discussion

Our study provides rare data on the establishment, growth and extinction of native plant patches in relation to the spread of an invasive plant species (for other exceptions see Huang and Zhang 2007; Rice et al. 2000). It also reveals consistently strong support for the hypothesis that invasive smooth brome is detrimental to the patch dynamics of prairie cordgrass. Not only are the growth rates of established cordgrass patches negatively related to the proportion of brome in the matrix surrounding each patch, but also areas dominated by brome ( $\geq 50\%$  coverage) are approximately 1.3 times less likely to be colonized by cordgrass and eight times more likely to have a



**Fig. 3** The mean  $\pm$  SE percent change in cordgrass patch size (see Methods) in relation to the percentage of brome within a 0.5 m buffer surrounding the cordgrass patch. For each site, the change in patch size is reported for three different time periods. The lines are fit by least-squares regression and are only intended to reveal trends in the data

cordgrass patch go extinct. Although our data are only correlative, we suggest that brome has a direct negative effect on cordgrass abundance. This conclusion is corroborated by the recent experimental work of Williams and Crone (2006) who demonstrated that smooth brome was capable of lowering survivorship and slowing the growth of native *Anemone patens*, a long-lived native perennial of North American grasslands. Furthermore, F. P. Dilleuth et al. (unpublished data) transplanted cordgrass seeds and seedlings into brome and cordgrass dominated habitats and found that growth rates and survivorship were lowest in brome. Our survey results, in combination with these experimental studies, support a large body of literature indicating that invasive plants are able to



**Fig. 4** Percentage of cordgrass patches that (a) became established or (b) went extinct in habitats consisting of a low (<50%) or high (>50%) percentage of brome. Separate bars are used for each time period

reduce abundances of native species in infested habitats (e.g., Keane and Crawley 2002; Mack et al. 2000).

Despite the negative association between brome occurrence and cordgrass patch dynamics, it is not clear that brome would eventually displace cordgrass in our study sites. From 2000 to 2004, cordgrass patches declined in size by an average 27 m<sup>2</sup> (16%), but between 2004 and 2006, cordgrass patches increased in size by 20 m<sup>2</sup> (12%) resulting in no net change in cordgrass patch size from 2000 to 2006. The decline in the first time period cannot be attributed solely to smooth brome because cordgrass patch sizes decreased in areas of high and low brome

coverage (although, it was greater for the former areas; see Fig. 2). The difference in cordgrass growth rates between 2000–2004 and 2004–2006 may be due to changes in precipitation levels. In 2000–2004, precipitation levels averaged 7% above the hundred year norm for the May–August growing season (National Climatic Data Center 2007). The period 2004–2005 was particularly wet and had precipitation levels 22% above the above the hundred year average. These heavy rains resulted in standing water across all of our field sites for much of the growing season. Cordgrass is more hydrophytic than most prairie plants (Sedivec and Barker 1998) and likely thrived under these conditions. The effects of this unusually wet period on cordgrass probably extended through the end of our study period.

Another reason why brome may not displace cordgrass is because of microhabitat differences in performance of both species. Although these prairie fragments are quite flat (<0.5 m elevational change), relatively low areas may favor cordgrass over brome. Our transplant experiment F. P. Dilleuth et al. (unpublished data) supports this assertion. Brome seedling transplants did poorer than cordgrass in low areas dominated by cordgrass, even when potential competition from cordgrass was removed. Given the spatial and temporal heterogeneity observed in these prairie habitats, the complete displacement of cordgrass by brome (at the scale of a prairie fragment) probably would require either an extended drought period, or the accretion of sediments by brome and the gradual elimination of low spots in the prairie. Our conclusion that invasive smooth brome is unlikely to cause the extinction of native prairie cordgrass is consistent with the current paradigm regarding invasive exotic species (Sax et al. 2002; Tilman 1997). For example, New Zealand has over 2,069 known successful exotic colonizers but only three known extinctions of native plants (Sax et al. 2005).

Through its effects on cordgrass patch growth and extinction-establishment dynamics, brome can have important consequences for cordgrass population dynamics. Once brome has gained a foothold in a habitat, it may represent a barrier to the spread of cordgrass (see Standish et al. 2001). If for example, dry conditions favor the spread of brome (Blankespoor and Larson 1994) into cordgrass habitat, it may be difficult for cordgrass to spread back into its

old habitat after wet (favorable) conditions return (Wilson et al. 2004). Also, as brome spreads across the prairie landscape it may fragment or cause the extinction of local stands of cordgrass and increase isolation among existing patches (Cronin 2007; Cronin and Haynes 2004; Haynes et al. 2007; Haynes and Cronin 2006). Isolation of cordgrass patches, coupled with a reduction in patch size, may increase the likelihood of inbreeding and strengthen Allee effects associated with small population size (Davis et al. 2004a, b).

Brome invasion is also likely to have effects that extend to higher trophic levels. For example, Cronin and his colleagues (Cronin 2003c, 2004, 2007; Cronin et al. 2004; Haynes and Cronin 2003, 2006) have explored the consequences of the invasion of smooth brome on the primary herbivore of cordgrass, the planthopper *Prokelisia crocea*, and the planthoppers specialist natural enemy, the parasitoid *Anagrus columbi*. Movement studies have revealed that planthoppers and parasitoids are more likely to emigrate from cordgrass patches embedded in a brome matrix than in native matrix habitat (Baum et al. 2004; Cronin and Haynes 2004; Haynes and Cronin 2003, 2006). Because of brome's effect on emigration behavior, local populations of *P. crocea* and *A. columbi* are reduced in density by 50% and are 4–5 times more likely to go extinct than in patches surrounded by native vegetation (Cronin and Haynes 2004). Moreover, at the landscape level, brome dominated landscapes can lead to the extinction of planthopper and parasitoid populations (Cronin 2007). As was recently demonstrated by Cronin (2007), by infiltrating cordgrass patches and diminishing patch area, brome may degrade cordgrass patch quality to the extent that patches pass from population sources to sieves and eventually to sinks. Finally, the parasitoid is far more sensitive than its host to the invasion of brome (with regard to all of the above parameters) (Cronin 2007; Cronin and Haynes 2004). This one detailed case study highlights the potential consequences that invasive plants may have on the remainder of community. Bottom-up effects, owing to invasive plant species, have been reported for other systems and reflect the complex direct and indirect interactions that may occur during the invasion process (Ellingson and Anderson 2002; Gerber et al. 2008; Gratton and Denno 2005).

## Brome management

The lack of a management plan for smooth brome can have dire consequences for dominant prairie plants (this study; Blankespoor and Larson 1994; Murphy and Grant 2005; Willson and Stubbendieck 2000; F. P. Dillemoth, unpublished data), and potentially many native arthropod species. Currently, management of smooth brome is limited because other invasive species (e.g., *Cirsium arvense*, Canada thistle; *Euphorbia esula*, leafy spurge and *Artemisia absinthium*, wormwood) have been given higher priority by local land managers (K. Tompkins, personal communication). However, land managers report some success in reducing the establishment, spread and abundance of smooth brome with the use of prescribed burns (Willson and Stubbendieck 2000). This type of management has been successful in previous habitats dominated by *Spartina* dominated habitats (see Feldman et al. 2004; Schmalzer et al. 1991). The basis for this management tactic is a model developed by Willson and Stubbendieck (2000) that recommends burning in early spring at the four or five leaf stage of smooth brome. This tactic is thought to work because smooth brome is a cool season grass that begins its growth cycle and sets seeds before native warm season grasses (i.e., prairie cordgrass). Therefore, a properly timed prescribed fire may reduce smooth brome abundance before it set seeds, while freeing up space and resources for native warm season grasses to flourish. According to Willson and Stubbendieck (2000), warm season grasses needed to respond and achieve a minimum of 20% coverage before the next year's growth cycle begins for this practice to effectively reduce smooth brome populations. Rigorous field testing of this management tactic has yet to be attempted. If fire is not an option, then land managers may have to rely on mechanical methods (tillage which may have to be repeated over several years), haying, grazing, or chemical treatment (K. Tompkins, personal communications 2008). Unfortunately, these latter approaches are likely to be more expensive and less ecologically sound than burning.

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## Reference

- Barbraud C, Nichols JD, Hines JE, Hafner H (2003) Estimating rates of local extinction and colonization in colonial species and an extension to the metapopulation and community levels. *Oikos* 101(1):113–126
- Bart D, Hartman JM (2000) Environmental determinants of *Phragmites australis* expansion in a New Jersey salt marsh: an experimental approach. *Oikos* 89:59–69. doi: [10.1034/j.1600-0706.2000.890107.x](https://doi.org/10.1034/j.1600-0706.2000.890107.x)
- Baum KA, Haynes KJ, Dillemoth FP, Cronin JT (2004) The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* 85:2671–2676. doi: [10.1890/04-0500](https://doi.org/10.1890/04-0500)
- Blankespoor GW, Larson EA (1994) Response of smooth brome (*Bromus inermis* Leys.) to burning under varying soil moisture conditions. *Am Midl Nat* 131(2):66–272
- Bradley BA, Mustard JF (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecol Appl* 16(3):1132–1147. doi: [10.1890/1051-0761\(2006\)016\[1132:CTLDOA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1132:CTLDOA]2.0.CO;2)
- Brown KA, Gurevitch J (2004) Long-term impacts of logging of forest diversity in Madagascar. *Proc Natl Acad Sci USA* 101:6045–6049. doi: [10.1073/pnas.0401456101](https://doi.org/10.1073/pnas.0401456101)
- Chaberrie O, Roulier FDR, Hoeblich HLN, Seberr-Cullier E, Closset-Kopp DB, Leblanc I, Jaminon JR, Decocq G (2007) Defining patch mosaic functional types to predict invasion patterns in a forest landscape. *Ecol Appl* 17(2):464–481
- Clavero M, Garcia-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends Ecol Evol* 20(3):110. doi: [10.1016/j.tree.2005.01.003](https://doi.org/10.1016/j.tree.2005.01.003)
- Cronin JT (2003a) Matrix heterogeneity and planthopper–parasitoid interactions in space. *Ecology* 84:1506–1516. doi: [10.1890/0012-9658\(2003\)084\[1506:MHAIH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1506:MHAIH]2.0.CO;2)
- Cronin JT (2003b) Movement and spatial population structure of a prairie planthopper. *Ecology* 84:1179–1188. doi: [10.1890/0012-9658\(2003\)084\[1179:MASPSO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[1179:MASPSO]2.0.CO;2)
- Cronin JT (2003c) Patch structure, oviposition behavior, and the distribution of parasitism risk. *Ecol Monogr* 73:283–300. doi: [10.1890/0012-9615\(2003\)073\[0283:PSOBAT\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2003)073[0283:PSOBAT]2.0.CO;2)
- Cronin JT (2004) Host–parasitoid extinction and colonization in a fragmented prairie landscape. *Oecologia* 139: 503–514. doi: [10.1007/s00442-004-1549-8](https://doi.org/10.1007/s00442-004-1549-8)
- Cronin JT (2007) From population sources to sieves: the matrix alters host–parasitoid source–sink structure. *Ecology* 88:2966–2976. doi: [10.1890/07-0070.1](https://doi.org/10.1890/07-0070.1)
- Cronin JT, Haynes KJ (2004) Invasive plants promote unstable host–parasitoid patch dynamics. *Ecology* 85:2772–2782. doi: [10.1890/04-0303](https://doi.org/10.1890/04-0303)
- Cronin JT, Haynes KJ, Dillemoth FP (2004) Spider effects on planthopper mortality, dispersal, and spatial population dynamics. *Ecology* 85:2134–2143. doi: [10.1890/03-0591](https://doi.org/10.1890/03-0591)

- D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu Rev Ecol Syst* 23:63–87
- Davis HG, Taylor CM, Civiile JC, Strong DR (2004a) An Allee effect at the front of a plant invasion: *Spartina* in a Pacific estuary. *J Ecol* 92:321–327. doi:10.1111/j.0022-0477.2004.00873.x
- Davis HG, Taylor CM, Lambrinos JG, Strong DR (2004b) Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proc Natl Acad Sci USA* 101:13804–13807. doi:10.1073/pnas.0405230101
- Delaune M, Chikinev M (2005) XTools Pro. DataEast company. <http://www.xtoolspro.com/index.html>
- Dyer AR, Rice KJ (1999) Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* 80:2697–2710
- Ehrenfeld JG (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–523. doi:10.1007/s10021-002-0151-3
- Ellingson AR, Anderson DC (2002) Spatial correlations of *Dicreoprocta apache* and its host plants: evidence for a negative impact from *Tamarix* invasion. *Ecol Entomol* 27:16–24. doi:10.1046/j.0307-6946.2001.00387.x
- Emery SM, Gross KL (2005) Effects of timing of prescribed fire on the demography of an invasive plant, *Centaurea maculosa* (spotted knapweed). *J Appl Ecol* 42:60–69. doi:10.1111/j.1365-2664.2004.00990.x
- Everitt JH, Alaniz MA, Escobar DE, Davis MR (1992) Using remote sensing to distinguish common (*Isocoma coronopifolia*) and Drummond goldenweed (*Isocoma drummondii*). *Weed Sci* 40:621–628
- Feldman SR, Bisaro V, Lewis JP (2004) Photosynthetic and growth responses to fire of the subtropical temperate grass, *Spartina argentinensis* Parodi. *Flora* 199(6):491–499
- Fisher RA (1937) The wave of advance of advantageous genes. *Ann Eugen* 7:355–369
- García-Robledo CA, Murcia C (2005) Comparative habitat susceptibility to invasion by Chinese ash (*Fraxinus chinensis*) in a tropical Andean landscape. *Biol Invasions* 7:405–415. doi:10.1007/s10530-004-2576-4
- Gerber E, Krebsa C, Murrell C, Morettib M, Rocklinc R, Schaffner U (2008) Exotic invasive knotweeds (*Fallopia* spp.) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biol Conserv* 141(3):646–654
- Gratton C, Denno RF (2005) Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*. *Restor Ecol* 13(2):358–372. doi:10.1111/j.1526-100X.2005.00045.x
- Gurevitch J, Scheiner SM, Fox GA (2002) The ecology of plants. Sinauer, Sunderland
- Haynes KJ, Cronin JT (2003) Matrix composition affects the spatial ecology of a prairie planthopper. *Ecology* 84:2856–2866. doi:10.1890/02-0611
- Haynes KJ, Cronin JT (2006) The role of the landscape matrix and patch edges on herbivore movement behavior. *Oikos* 113:43–54. doi:10.1111/j.0030-1299.2006.13977.x
- Haynes KJ, Dilleuth FP, Anderson B, Hakes A, Jackson HB, Cronin JT (2007) Patch geography surpasses patch quality in its effects on herbivore dispersal and distribution. *Oecologia* 151:431–441. doi:10.1007/s00442-006-0600-3
- Hengeveld R (1989) Dynamics of biological invasions. Chapman and Hall, London
- Hitchcock AS (1963) Manual of the grasses of the United States. Dover Publications, New York
- Hodkinson DJ, Thompson K (1997) Plant dispersal: the role of man. *J Appl Ecol* 34(6):1484–1496. doi:10.2307/2405264
- Huang H, Zhang L (2007) A study of the population dynamics of *Spartina alterniflora* at Jiuduansha shoals, Shanghai, China. *Ecol Eng* 29(2):164–172
- Johnson DM, Liebhold AM, Tobin PC, Bjørnstad ON (2006) Allee effects and pulsed invasion by the gypsy moth. *Nature* 444:361–363. doi:10.1038/nature05242
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol Evol* 17(4):164–170. doi:10.1016/S0169-5347(02)02499-0
- Kowarik I (2003) Human agency in biological invasions: secondary releases foster naturalization and population expansion of alien plant species. *J Biol Invasions* 5(4):293–312
- Larson DL, Anderson PJ, Newton W (2001) Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecol Appl* 11:128–141. doi:10.1890/1051-0761(2001)011[0128:APIIMG]2.0.CO;2
- Lass LW, Prather TS, Glenn NF, Wass LW, Weber KT, Mundt JT, Pettingill J (2005) A review of remote sensing of invasive weeds and example of the early detection of spotted knapweed (*Centaurea maculosa*) and babysbreath (*Gypsophila paniculata*) with a hyperspectral sensor. *Weed Sci* 53:242–251
- Mack RN, Simberloff D, Lonsdale WM (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10(3):689–710. doi:10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2
- Mack MC, D'Antonio CM, Ley RE (2001) Alteration of ecosystem nitrogen dynamics by exotic plants: a case study of C-4 grasses in Hawaii. *Ecol Appl* 11:1323–1335
- Madden M (2004) Remote sensing and geographic information system operations for vegetation mapping of invasive exotics. *Weed Technol* 18:1457–1463
- Mladinich CS, Bustos MR, Stitt S, Root R, Brown K, Anderson GL et al (2006) The use of Landsat 7 enhanced thematic mapper plus for mapping leafy spurge. *Rangeland Ecol Manag* 59:500–506. doi:10.2111/06-027R1.1
- Mooney HA, Hamburg SP, Drake JA (1986) The invasions of plants and animals into California. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Ecological studies. Springer-Verlag, New York, pp 250–274, 321
- Murphy RK, Grant TA (2005) Land management history and floristics in mixed-grass prairie, North Dakota, USA. *Nat Areas J* 25(4):351–358
- National Climatic Data Center, US Department of Commerce. <http://cdo.ncdc.noaa.gov/cgi-bin/cdo/cdoprod.pl>. Accessed 26 Feb 2007
- Nernberg D, Dale MRT (1997) Competition of five native prairie grasses with *Bromus inermis* under three moisture regimes. *Can J Bot (Revue Canadienne De Botanique)* 75:2140–2145
- North Dakota Department of Agriculture (2007) North Dakota noxious weed list. <http://www.agdepartment.com/noxiousweeds/searchweeds.asp>

- Otfinowski R, Kenkel NC, Catling PM (2007) The biology of Canadian weeds. 134. *Bromus inermis* Leys. Can J Plant Sci 87:183–198
- Pengra BW, Johnston CA, Loveland TR (2007) Mapping an invasive plant, *Phragmites australis*, in coastal wetlands using the EO-1 Hyperion hyperspectral sensor. Remote Sens Environ 108:74–81. doi:10.1016/j.rse.2006.11.002
- Rice D, Rooth J, Stevenson JC (2000) Colonization and expansion of *Phragmites australis* in upper Chesapeake Bay tidal marshes. Wetlands 20(2):280–299. doi:10.1672/0277-5212(2000)020[0280:CAEOPA]2.0.CO;2
- Samson FB, Knopf FL, Ostlie WR (2004) Great Plains ecosystems: past, present, and future. Wildl Soc Bull 32:6–15. doi:10.2193/0091-7648(2004)32[6:GPEPPA]2.0.CO;2
- Sax DF, Gaines SD, Brown JH (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. Am Nat 160:766–783. doi:10.1086/343877
- Sax DF, Stachowicz JJ, Gaines SD (2005) Species invasions—insights into ecology, evolution and biogeography. Sinauer, Sunderland
- Schmalzer PA, Hinkle CR, Mailander JL (1991) Changes in community composition and biomass in *Juncus-roemerianus* Scheele and *Spartina bakeri* Merr marshes one year after a fire. Wetlands 11(1):67–86
- Seabloom EW, Williams JW, Slayback D, Stoms DM, Viers JH, Dobson AP (2006) Human impacts, plant invasion, and imperiled plant species in California. Ecol Appl 16(4):1338–1350
- Sedivec KT, Barker WT (1998) Selected North Dakota and Minnesota range plants NDSU Ext Ser. North Dakota State University, Fargo
- Simmons MT, Windhager S, Power P, Lott J, Lyons RK, Schwoppe C (2007) Selective and non-selective control of invasive plants: the short-term effects of growing-season prescribed fire, herbicide, and mowing in two Texas prairies. Restor Ecol 15(4):662–669
- Skellam JG (1951) Random dispersal in theoretical populations. Biometrika 38:196–218
- Standish RJ, Robertson AW, Williams PA (2001) The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration. J Appl Ecol 38(6):1253–1263. doi:10.1046/j.0021-8901.2001.00673.x
- Stohlgren TJ, Bull KA, Otuski Y, Villa CA, Lee M (1998) Riparian zones as havens for exotic plant species in the central grasslands. Plant Ecol 138:113–125. doi:10.1023/A:1009764909413
- Stoner KJL, Joern A (2004) Landscape vs. local habitat scale influences to insect communities from tallgrass prairie remnants. Ecol Appl 14(5):1306–1320. doi:10.1890/03-5112
- Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. New Phytol 176:256–273. doi:10.1111/j.1469-8137.2007.02207.x
- Thomson D (2005) Measuring the effects of invasive species on the demography of a rare endemic plant. Biol Invasions 7:615–624. doi:10.1007/s10530-004-5853-3
- Tilman D (1997) Mechanisms of plant competition. In: Crawley M (ed) Plant ecology, 2nd edn. Blackwell Science, Oxford, pp 239–261
- United States Department of Agriculture and Natural Resource Conservation Service (2008) The PLANTS database (<http://plants.usda.gov>, Jan 17 2008). National Plant Data Center, Baton Rouge, LA, USA
- U.S. Fish and Wildlife Service (2007) Kellys Slough National Wildlife Refuge Devils Lake, North Dakota. [www.fws.gov/devilslake/kellys\\_slough](http://www.fws.gov/devilslake/kellys_slough)
- Vitousek PM (1997) Human domination of earth's ecosystems. Science 278:21–21
- Vitousek PM, Walker LR (1989) Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. Ecol Monogr 59:247–265. doi:10.2307/1942601
- Weston LA, Duke SO (2003) Weed and crop allelopathy. Crit Rev Plant Sci 22(3–4):367–389. doi:10.1080/713610861
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48:607–615. doi:10.2307/1313420
- Williams JL, Crone EE (2006) The impact of invasive grasses on the population growth of *Anemone patens*, a long-lived native forb. Ecology 87:3200–3208. doi:10.1890/0012-9658(2006)87[3200:TIOIGO]2.0.CO;2
- Willson GD, Stubbendieck J (2000) A provisional model for smooth brome management in degraded tallgrass prairie. Ecol Res 18(1):34–38
- Wilson MV, Ingersoll CA, Wilson MG, Clark DL (2004) Why pest plant control and native plant establishment failed: a restoration autopsy. Nat Areas J 24(1):23–31
- Wiser SK, Allen RB, Clinton PW, Platt KH (1998) Community structure and forest invasion by an exotic herb over 23 years. Ecology 79(6):2071–2081