

# Using ecological restoration to constrain biological invasion

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## Summary

1. Biological invasion can permanently alter ecosystem structure and function. Invasive species are difficult to eradicate, so methods for constraining invasions would be ecologically valuable. We examined the potential of ecological restoration to constrain invasion of an old field by *Agropyron cristatum*, an introduced C<sub>3</sub> grass.

2. A field experiment was conducted in the northern Great Plains of North America. One-hundred and forty restored plots were planted in 1994–96 with a mixture of C<sub>3</sub> and C<sub>4</sub> native grass seed, while 100 unrestored plots were not. Vegetation on the plots was measured periodically between 1994 and 2002.

3. *Agropyron cristatum* invaded the old field between 1994 and 2002, occurring in 5% of plots in 1994 and 66% of plots in 2002, and increasing in mean cover from 0.2% in 1994 to 17.1% in 2002. However, *A. cristatum* invaded one-third fewer restored than unrestored plots between 1997 and 2002, suggesting that restoration constrained invasion. Further, *A. cristatum* cover in restored plots decreased with increasing planted grass cover. Stepwise regression indicated that *A. cristatum* cover was more strongly correlated with planted grass cover than with distance from the *A. cristatum* source, species richness, percentage bare ground or percentage litter.

4. The strength of the negative relationship between *A. cristatum* and planted native grasses varied among functional groups: the correlation was stronger with species with phenology and physiology similar to *A. cristatum* (i.e. C<sub>3</sub> grasses) than with dissimilar species (C<sub>4</sub> grasses).

5. Richness and cover of naturally establishing native species decreased with increasing *A. cristatum* cover. In contrast, restoration had little effect on the establishment and colonization of naturally establishing native species. Thus, *A. cristatum* hindered colonization by native species while planted native grasses did not.

6. *Synthesis and applications.* To our knowledge, this study provides the first indication that restoration can act as a filter, constraining invasive species while allowing colonization by native species. These results suggest that resistance to invasion depends on the identity of species in the community and that restoration seed mixes might be tailored to constrain selected invaders. Restoring areas before invasive species become established can reduce the magnitude of biological invasion.

*Key-words:* *Agropyron cristatum*, functional groups, mixed-grass prairie, old field, succession

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## Introduction

Biological invasion can produce profound and irreversible changes to ecosystem structure and function (Mooney &

Hobbs 2000; Sakai *et al.* 2001). *Agropyron cristatum* (L.) Gaertn., a perennial C<sub>3</sub> grass, is a model species illustrating these effects. Introduced to North America in the early 1900s, *A. cristatum* now dominates 13–17 million ha of semi-arid grassland on the continent (Heidinger & Wilson 2002). Stands dominated by *A. cristatum* contain 35% lower species richness (Heidinger & Wilson 2002) and 25% less soil carbon (Christian & Wilson 1999) than native grassland.

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Invasive species are difficult to eradicate once established (Benz *et al.* 1999; Manchester & Bullock 2000; Wilson 2002; Price & Weltzin 2003). Methods of preventing or constraining their spread have been difficult to develop (Keane & Crawley 2002; Perry & Galatowitsch 2003; Perry, Galatowitsch & Rosen 2004) but would be ecologically valuable. Our objective was to explore the potential of ecological restoration to constrain the spread of invasive species in old fields. Ecological restoration is 'the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed' (SER 2002) and often involves the planting of native species associated with later successional stages. Negative correlations between abundances of native and introduced species (Anderson & Inouye 2001; Heidinga & Wilson 2002) suggest that invasion by *A. cristatum* could be reduced if old fields were planted with native perennial grasses from later successional stages.

*Agropyron cristatum* alters the successional trajectories of ecosystems where it is established: old fields sown with *A. cristatum* half a century ago remain dominated by this species, whereas unsown old fields now resemble native grassland (Christian & Wilson 1999). Preferred management actions to constrain invasion by *A. cristatum* should have minimal effects on other species. We assessed this by examining the effects of invasion and restoration on the species richness and cover of naturally establishing (non-planted) native species.

Interspecific differences in resource use and other traits suggest that native species should differ in their effectiveness in constraining invasion. Differences are likely to be most pronounced among functional groups (species with similar phenologies and physiologies). In general, established (resident) vegetation should have a stronger inhibitory effect on invading species from the same functional group than on species from other functional groups (Fargione, Brown & Tilman 2003). We hypothesized that effectiveness in constraining invasion by *A. cristatum* would differ among functional groups and would be greater in restored vegetation from the same functional group as *A. cristatum* ( $C_3$  grasses) than in restored vegetation from another functional group ( $C_4$  grasses).

We also examined the relative importance of biotic- and dispersal-related variables to the spread of *A. cristatum*. Variables thought to be potentially important included cover of planted grasses, percentage bare ground, percentage litter, species richness, distance from the *A. cristatum* source and distance parallel to the prevailing wind. Here we report on a 9-year field experiment that examined these factors.

### Materials and methods

We studied an old field in Grasslands National Park, Saskatchewan, Canada (49°11'N 107°43'W). The field was cultivated for more than 30 years and abandoned

in 1984. A roadside 20 m south of the experiment was dominated by a well-established stand of *A. cristatum* when our experiment began in 1994. Wilson *et al.* (2004) provide details of the experimental design and describe native grass establishment through to 1997. We examined invasion of the experiment by *A. cristatum* between 1994 and 2002. Two-hundred and forty plots, each 3 × 10 m, were randomly assigned to treatments. One-hundred and forty plots were planted and are referred to as restored plots; the remaining 100 plots were not planted and are referred to as unrestored plots. Restored plots were planted by broadcasting or drilling seed of a mixture of native grasses (*Bouteloua gracilis*, *Hesperostipa comata*, *Koeleria macrantha*, *Elymus lanceolatus* and *Pascopyrum smithii*) or by spreading seed cleanings (biomass remaining after processing to remove awns from *Hesperostipa comata* seed) that contained seeds of several native species. *Bouteloua gracilis* has a  $C_4$  photosynthetic pathway; the other planted grass species have  $C_3$  photosynthetic pathways. Nomenclature follows USDA, NRCS (2004).

Plant cover was measured annually during 1994–97 and again in 2002. All measurements were made in the centre 0.5 × 1 m of each plot. For each species, we estimated cover using Daubenmire's (1959) cover classes, with the addition of a 0–1% class to more accurately estimate the cover of small and infrequent species.

We used contingency analysis to determine whether the rate of invasion by *A. cristatum* differed between restored and unrestored plots. We restricted our focus in this analysis to invasion between 1997 and 2002 so that native grasses had at least 2 years to establish before invasion. The contingency analysis compared the restored and unrestored plots with respect to the proportion of plots where *A. cristatum* was absent in 1997 but present in 2002.

Next, we focused on the restored plots in 2002 and used regression to examine the relationship between *A. cristatum* cover and several biotic and dispersal-related variables: cover of planted grasses, species richness, percentage bare ground, percentage litter, distance from the *A. cristatum* source and distance east in the site (the prevailing wind is from the west). Species cover and richness were included because they are likely to vary with the abundance of an invader (Anderson & Inouye 2001). Bare ground and litter were included as variables that might affect seedling establishment. Cover values were arcsin (square-root  $x$ ) transformed and richness data were log ( $x + 1$ ) transformed for analysis; statistics were back-transformed for presentation. Plots with zero values for both variables were omitted from analyses. We then used stepwise regression to assess the relative importance of variables. Variables were included in the model if  $P \leq 0.05$  and removed if  $P > 0.10$ . Standard coefficients were used to make comparisons among variables included in the stepwise regression.

To test whether the response of *A. cristatum* cover varied with functional group identity, we followed the

regression of *A. cristatum* cover against planted grass cover with separate regressions of *A. cristatum* cover against cover of planted C<sub>3</sub> grasses and against cover of planted C<sub>4</sub> grasses.

We also tested the correlations between the cover of naturally establishing (i.e. non-planted) native species and the covers of *A. cristatum* and planted native species. This analysis was repeated for richness of naturally establishing species.

## Results

### SPREAD OF *A. CRISTATUM*

*Agropyron cristatum* occurred in 5% of plots in 1994, 34% in 1997 and 66% in 2002. Mean cover of *A. cristatum* was 0.2% in 1994, 2.2% in 1997 and 17.1% in 2002. As *A. cristatum* invaded the plots over the course of the experiment, differences in its presence and abundance among treatments reflected differences in its ability to invade treatments. Invasion during 1997–2002, after native grasses had established, was significantly lower in restored plots (28% of plots invaded) than in unrestored plots (42% of plots invaded;  $Z = 2.27$ ,  $P = 0.011$ ). Thus, restoration reduced the spread of *A. cristatum* by one-third. *Agropyron cristatum* cover ranged from 0 to 100% of the total plant cover in individual plots in 2002.

### SUCCESSIONAL DYNAMICS

Accompanying the spread of *A. cristatum* between 1994 and 2002 were additional changes indicating a transition in dominance from ruderal to perennial species. Two annual forbs, *Kochia scoparia* and *Conyza canadensis*, accounted for > 50% of the plant cover in 1994 in both restored and unrestored plots (Table 1). By 1997, *Kochia scoparia* was absent from the plots, *Conyza canadensis* accounted for < 3% of the plant

cover and plots were dominated by *Elymus lanceolatus*, other planted native grasses (restored plots only), *A. cristatum*, *Lactuca serriola*, *Tragopogon dubius* and *Hordeum jubatum*. Of these species, only planted native grasses and *A. cristatum* remained abundant in 2002.

In restored plots, perennial grasses increased dramatically in importance. The proportion of plant cover attributable to grasses increased from 8.5% in 1994 to 79.2% in 2002 (Fig. 1). Planted native grasses, particularly *Elymus lanceolatus*, *Bouteloua gracilis* and *Koeleria macrantha*, comprised > 40% of the plant cover in restored plots in 2002 (Table 1). Restoration success varied among plots: cover of planted native grasses in 2002 ranged from 0 to 100% of total plant cover in restored plots.

*Agropyron cristatum* was the most abundant species in unrestored plots in 2002, but grasses as a whole were less prevalent than in restored plots: the proportion of plant cover attributable to grasses increased from 6.0% in 1994 to 44.0% in 2002 (Fig. 1). Short-lived perennial forbs such as *Taraxacum officinale* and *Medicago sativa* were the next most abundant species in these plots, followed by *Elymus lanceolatus* (Table 1).

### CORRELATIONS BETWEEN *A. CRISTATUM* AND BIOTIC- AND DISPERSAL-RELATED VARIABLES

In restored plots in 2002, cover of *Agropyron cristatum* decreased significantly with increasing total cover of planted native grasses (Fig. 2a). *A. cristatum* cover was more strongly negatively correlated with planted C<sub>3</sub> grass cover than with planted C<sub>4</sub> grass cover (Fig. 2b,c), indicating that functional groups differed in their ability to resist *A. cristatum* invasion.

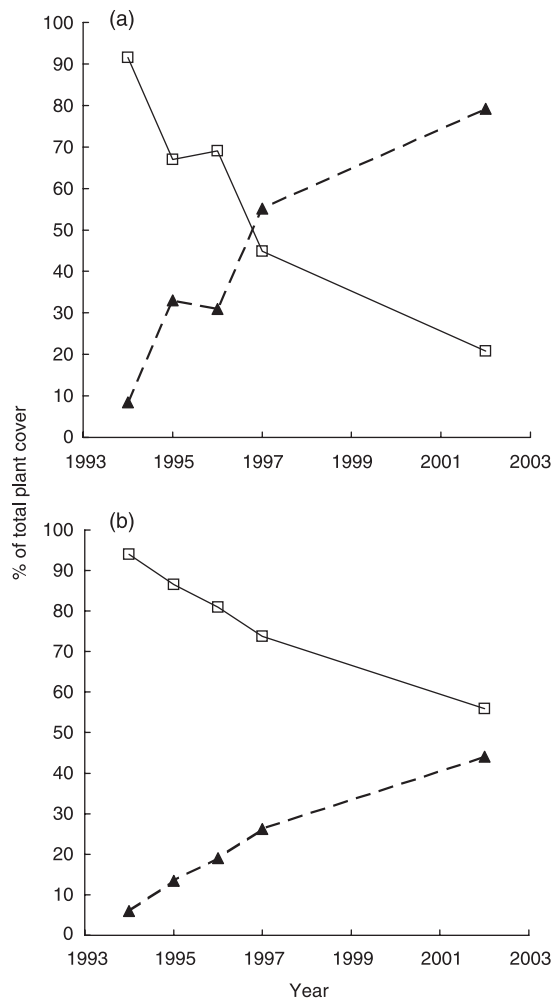
*Agropyron cristatum* cover decreased significantly with distance from the *A. cristatum* source ( $F_{1,138} = 16.09$ ,  $P < 0.0001$ ; data not shown) but not with distance

**Table 1.** Dominant species (percentage of total plant cover) and total plant cover (mean) in restored and unrestored plots in 1994, 1997 and 2002. The growth form (G, grass; F, forb) and origin (I, introduced; N, native to North America) of each species are noted

Species	Growth form	Origin	Restored plots			Unrestored plots		
			1994	1997	2002	1994	1997	2002
<i>Agropyron cristatum</i>	G	I	0.4	10.1	30.3	1.2	9.7	29.6
<i>Bouteloua gracilis</i>	G	N	7.7	9.7	14.0	0.0	0.0	0.2
<i>Conyza canadensis</i>	F	N	23.8	2.1	0.0	32.1	2.5	0.0
<i>Elymus lanceolatus</i>	G	N	0.0	7.8	22.2	0.0	0.1	8.9
<i>Hordeum jubatum</i> *	G	N	0.2	8.8	0.1	4.0	13.8	1.4
<i>Kochia scoparia</i>	F	I	31.3	0.0	0.0	31.5	0.0	0.1
<i>Koeleria macrantha</i>	G	N	0.0	6.6	5.7	0.0	0.1	1.3
<i>Lactuca serriola</i>	F	I	16.8	20.1	0.0	17.3	27.5	0.0
<i>Medicago sativa</i>	F	I	0.1	0.7	7.4	0.0	0.1	15.7
<i>Taraxacum officinale</i>	F	N/I†	0.6	3.5	4.3	0.0	6.0	19.9
<i>Tragopogon dubius</i>	F	I	1.6	8.0	0.4	2.9	17.9	3.3
Total plant cover (%)			44.2	23.9	65.7	42.9	21.0	55.4

\**Hordeum jubatum* is a native early successional grass species and was not planted onto these plots.

†Origin uncertain according to USDA, NRCS (2004).

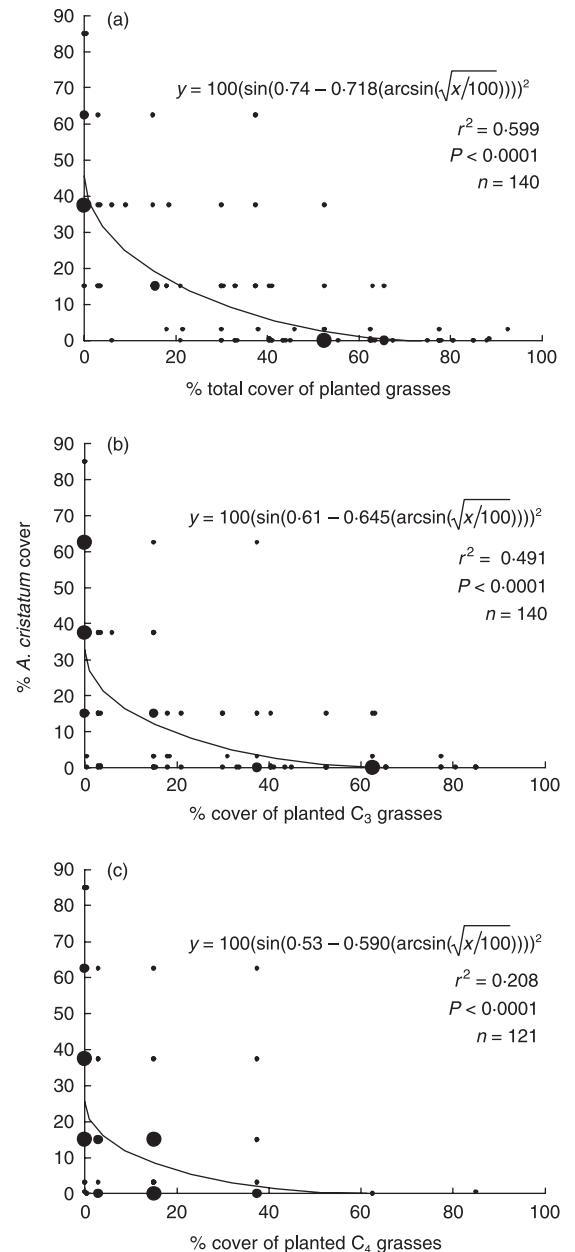


**Fig. 1.** Relative proportions of grasses and forbs (dashed and solid lines, respectively) in (a) restored and (b) un-restored plots in an old field in the northern Great Plains, North America, from 1994 to 2002.

parallel to the prevailing winds ( $F_{1,138} = 2.57$ ,  $P = 0.111$ ; data not shown). *Agropyron cristatum* cover was negatively correlated with species richness ( $F_{1,138} = 33.58$ ,  $P < 0.0001$ ; data not shown), negatively correlated with percentage bare ground ( $F_{1,135} = 3.96$ ,  $P = 0.049$ ; data not shown) and positively correlated with percentage litter ( $F_{1,138} = 7.87$ ,  $P = 0.006$ ; data not shown). However, stepwise regression indicated that neither dispersal nor biotic-related variables were included in the best-fitting model.

The best-fitting stepwise model ( $r^2 = 0.66$ ,  $F_{2,134} = 128.33$ ,  $P < 0.0001$ ) indicated that *A. cristatum* cover was negatively correlated with planted grass cover and percentage bare ground. The standardized coefficient for planted grass cover ( $-0.798$ ) was more than three times as large as that for percentage bare ground ( $-0.258$ ), showing that planted grass cover explained more of the variation in *A. cristatum* cover than any other variable.

Both functional groups were significantly correlated with *A. cristatum* cover when total planted grass cover was removed and planted  $C_3$  grass cover and planted  $C_4$



**Fig. 2.** Regressions between *Agropyron cristatum* cover and (a) total cover of planted native grasses, (b) cover of planted  $C_3$  grasses and (c) cover of planted  $C_4$  grasses in restored plots in an old field in the northern Great Plains, North America. Point size is proportional to the number of plots with that combination of values (small, 1–5; medium, 6–10; large, >10 plots). Cover data were arcsin square-root transformed for analysis; regression equations and lines were back-transformed to the original scale for presentation.

grass cover were included as potential variables in the stepwise regression. In this case, the best fitting stepwise model explained the same amount of variation ( $r^2 = 0.67$ ,  $F_{3,117} = 90.46$ ,  $P < 0.0001$ ) and indicated that *A. cristatum* cover was negatively correlated with planted  $C_3$  grass cover, planted  $C_4$  grass cover and percentage bare ground (standardized coefficients  $-0.763$ ,  $-0.357$  and  $-0.253$ , respectively). Thus, planted  $C_3$  grass cover explained more of the variation in *A. cristatum* cover than any other variable.

EFFECTS OF *A. CRISTATUM* AND PLANTED  
GRASSES ON NATURALLY ESTABLISHING  
NATIVE SPECIES

Total cover of naturally establishing native species was negatively correlated with *A. cristatum* cover (Fig. 3a) but did not vary significantly with planted grass cover (Fig. 3b). Species richness of naturally establishing native species was negatively correlated with *A. cristatum* cover (Fig. 3c) and with planted grass cover (Fig. 3d). However, the regression with *A. cristatum* explained much more of the variation in species richness than the regression with planted grass cover ( $r^2 = 0.26$  and  $0.07$ , respectively; Fig. 3c,d). Also, the slope of the best-fit line was steeper with *A. cristatum* cover than with planted grass cover as the independent variable.

## Discussion

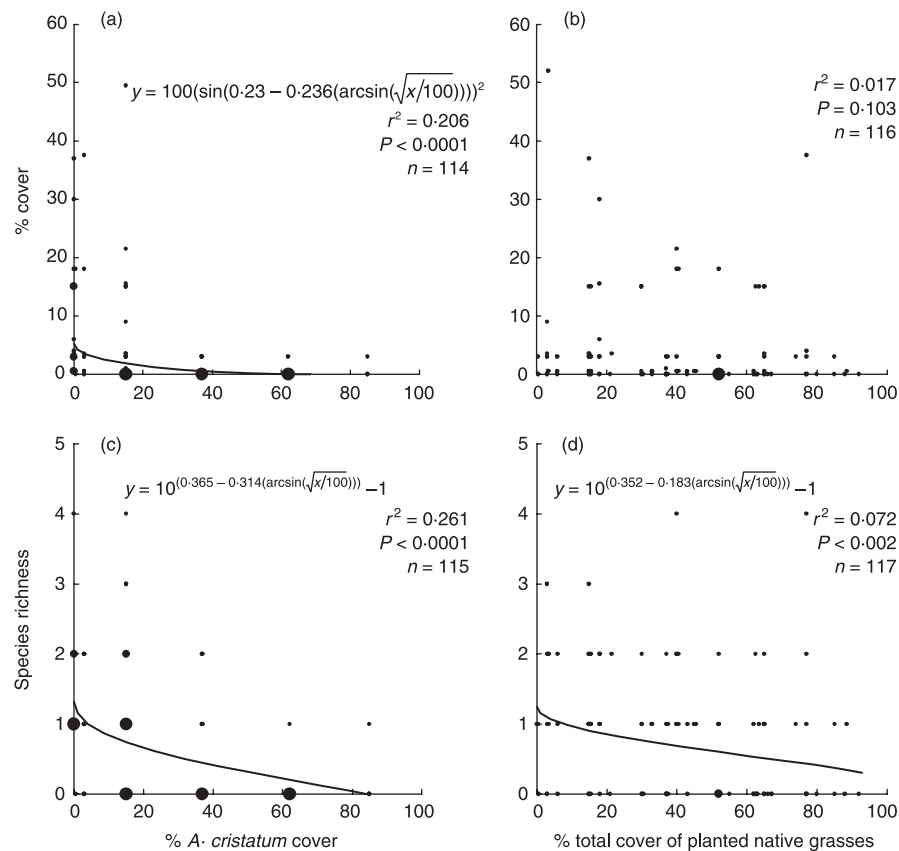
Ecological restoration is well-recognized for its beneficial effects with respect to soil stabilization, wildlife habitat and biodiversity. Our study suggests that another benefit of ecological restoration is that it can constrain biological invasion. While other studies have shown that ecological restoration can reduce the prevalence of established invasive species (Benz *et al.* 1999; Price & Weltzin 2003), this is the first study showing that

ecological restoration reduces the spread of an invasive species while permitting native species to establish.

Our analysis of invasion by *A. cristatum* was restricted to the period 1997–2002, after native grasses had had at least 2 years to establish. This allowed us to examine the invasion of *A. cristatum* into established stands of native species. While the pre-emptive establishment of native species may not be possible in all restorations, our results indicate that early establishment of native species can reduce future invasions.

By 2002, grass cover in the restored plots (Fig. 1) approached that of undisturbed prairie ( $> 80\%$ ; Coupland 1950). *Bouteloua gracilis* dominated the restored plots in the years immediately following planting (Wilson *et al.* 2004) but by 2002 was replaced by *Elymus lanceolatus* as the dominant planted grass. *Elymus lanceolatus* was absent from plots at the beginning of the experiment but by 2002 was spreading from restored into unrestored plots (Table 1).

Classical explanations of invasion rely on distance and dispersal vectors (Moody & Mack 1988). Stepwise regression indicated that these variables were not significant when planted grass covers were included as explanatory variables. Further, the  $F$ -value for the simple regression involving distance from the *A. cristatum* seed source was less than one-tenth the size of that for the regression with planted grass cover ( $F = 16$  and



**Fig. 3.** Regressions between total cover (top) and species richness (bottom) of naturally establishing native species and *Agropyron cristatum* cover (a, c) and total cover of planted native grasses (b, d). Point size is proportional to the number of plots with that combination of values (small, 1–5; medium, 6–10; large, >10 plots). Cover data were arcsin square-root transformed and species richness data were  $\log(x + 1)$  transformed for analysis; regression equations and lines were back-transformed to the original scale for presentation.

206, respectively). Presumably, the planted native species constrain invasion by pre-empting space and resources; biological pre-emption had a much greater negative effect on *A. cristatum* than dispersal-related variables did. These results suggest that ecological restoration may be able to override classical invasion factors.

Other field experiments suggest that invasibility is negatively correlated with diversity (van Ruijven, De Deyn & Berendse 2003). In this study, however, *A. cristatum* cover was much more strongly negatively correlated with planted grass cover ( $r^2 = 0.599$ ; Fig. 2a) than with species richness ( $r^2 = 0.196$ ). This suggests that resistance to invasion is not simply a linear function of species richness: species differ in how effective they are at constraining invasion. In particular, comparisons among functional groups (Fig. 2b,c) suggest that species from the same functional group (i.e. with similar phenology and physiology) will be more effective than dissimilar species at constraining an invasive species. This supports the idea that successful invaders replace native species in their niches rather than invading empty niches (Shea & Chesson 2002). This further implies that restoration seed mixes can be tailored to constrain selected invaders.

Restoration seed mixes cannot contain all species, however, so colonization by naturally establishing native species is necessary. Ideally, this colonization should not be hindered by the presence of the planted species. This was the case here, because the planted native grasses had little effect on the cover or richness of naturally establishing native species (Fig. 3b,d). Thus, ecological restoration functioned as a filter that allowed native species to establish at this site while reducing the spread of an invasive species. Restoration therefore can help address this most difficult aspect of invasion management (Keane & Crawley 2002).

Restoration success, as measured by planted grass cover, varied greatly among plots. The inverse relationship between restoration success and *A. cristatum* (Fig. 2) explains why *A. cristatum* had a high mean cover in restored plots (Table 1). The restored plots were located within an old field that, apart from our experimental plots, was not planted with native grasses. Restoration of larger contiguous areas might further constrain invasion by *A. cristatum*. However, optimal restoration methods vary temporally and at larger spatial scales (i.e. among sites) (Bakker *et al.* 2003; Wilson *et al.* 2004). Methods that are effective in one habitat may be less effective elsewhere.

As noted above, *A. cristatum* was present in restored plots, although at lower levels than in unrestored plots. Elimination of established *A. cristatum* plants requires intense management strategies aimed at halting seed production (Ambrose & Wilson 2003). The optimal management methods for an invasive species should capitalize on unique life-history characteristics of the species. For example, we have utilized the early growth and tall growth form of *A. cristatum* to apply systemic herbicide in a manner that kills it without affecting the

rest of the plant community (Bakker *et al.* 2003). Optimal management methods may also vary among habitats (Sheppard *et al.* 2002).

Because little is known of competitive relationships among native and introduced long-lived perennial species (Pyke & Archer 1991; Bakker & Wilson 2001), we need to determine how to maximize invader control. Topics such as the optimal establishment density of planted grasses and long-term population dynamics of native and invasive species demand attention. Other areas of concern include the eradication of established introduced species (Bakker *et al.* 2003) and the prevention of invasion into undisturbed systems (Heidinger & Wilson 2002). Experiments should be conducted in other ecosystems and with other invasive species and functional groups to assess the generality of the relationship between restoration and invasion described here.

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