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ORIGINAL PAPER

Using prairie restoration to curtail invasion of Canada thistle: the importance of limiting similarity and seed mix richness

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Abstract Theory has predicted, and many experimental studies have confirmed, that resident plant species richness is inversely related to invisibility. Likewise, potential invaders that are functionally similar to resident plant species are less likely to invade than are those from different functional groups. Neither of these ideas has been tested in the context of an operational prairie restoration. Here, we tested the hypotheses that within tallgrass prairie restorations (1) as seed mix species richness increased, cover of the invasive perennial forb, Canada thistle (*Cirsium arvense*) would decline; and (2) guilds (both planted and arising from the seedbank) most similar to Canada thistle would have a larger negative effect on it than less similar guilds. Each hypothesis was tested on six former agricultural fields restored to tallgrass prairie in 2005; all were within the tallgrass prairie biome in Minnesota, USA. A mixed-model with repeated measures (years) in a randomized block (fields) design indicated that seed mix richness had no effect on cover of Canada thistle. Structural equation models assessing effects of cover of each planted and non-planted

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guild on cover of Canada thistle in 2006, 2007, and 2010 revealed that planted Asteraceae never had a negative effect on Canada thistle. In contrast, planted cool-season grasses and non-Asteraceae forbs, and many non-planted guilds had negative effects on Canada thistle cover. We conclude that early, robust establishment of native species, regardless of guild, is of greater importance in resistance to Canada thistle than is similarity of guilds in new prairie restorations.

Keywords Tallgrass prairie · Restoration · *Cirsium arvense* · Limiting similarity · Species richness

Introduction

Tallgrass prairie restoration is increasingly being advocated as a method to reduce invasive species abundance and spread in former agricultural fields (Blumenthal et al. 2003, 2005; Middleton et al. 2010). By preempting light and nutrients, a successful prairie restoration leaves few resources for invaders. Nonetheless, invasive species are a common problem in restorations (Norton 2009), especially at the beginning (Quistberg and Stringham 2010) and their control can be a major component of restoration maintenance (Rowe 2010).

Canada thistle (*Cirsium arvense* (L.) Scop.), which occurs on the noxious weed lists of 33 states in the US (USDA Plants database, Plants.USDA.gov, accessed 18 March 2011), is one of the most troublesome weeds worldwide (Tiley 2010) and commonly invades restored prairies in the Midwestern US. Canada thistle is a deep-rooted perennial that produces extensive rhizomes. It is shade intolerant and seedlings compete poorly with other vegetation, so most spread is thought to be vegetative (Donald 1990) although this has been questioned (Heimann and Cussans 1996). Very small (2 cm) root fragments (rhizomes) are capable of producing new vegetative shoots (Nadeau and Vanden Born 1989), so plowing may spread propagules widely across a field. New prairie restorations are typically mowed to reduce light and moisture competition and prevent seed production from annuals, but mowing of the main shoot of Canada thistle stimulates sprouting from other root buds, so that more vegetative stems are produced. Furthermore, nitrogen concentrations are often high in fertilized agricultural fields in the Midwestern US (McLauchlan 2006) and shoot production of established Canada thistle clones is positively correlated with nitrogen availability in soils (Hamdoun 1970). Clearly, characteristics of Canada thistle ecology predispose it to being troublesome in prairie restoration. As a noxious weed, control of Canada thistle is mandated, yet control methods may harm planted species as well as invasives (Rinella et al. 2009).

Species diversity has been documented to decrease invasibility (Dukes 2001; Roscher et al. 2009; Tilman 1997), although these studies involved invasion into established vegetation stands, not new restorations. In the context of restoration of tallgrass prairie vegetation on former cropland, budgets typically limit the diversity of the seed mix and the question becomes, within affordable levels of seed mix richness, does resistance to invasion vary? The practitioner needs to know if planting more seeds of each species (i.e., increasing propagule pressure per species) is a better strategy to limit invasive species such as Canada thistle, than is increasing richness of the seed mix at the expense of declining propagule pressure per species. In addition to the planted species, restorations on former cropland will also harbor populations of native and non-native ruderals derived from the seed bank. The effects these non-planted components of species diversity may have on a targeted exotic perennial have not been assessed.

In their review of community assembly, Funk et al. (2008) suggested that by designing restored plant communities that have functional attributes similar to those of potential invaders, the invaders could be effectively excluded. Likewise, Brown (2004) advocated the use of functional guilds as the building blocks of restorations. Fargione et al. (2003) found that the more abundant a functional guild (e.g., cool- or warm-season grasses, forbs, legumes) was in an experimental plot, the less successful were invaders from that functional guild. Fargione and Tilman (2005) demonstrated the importance of differing phenology and rooting depth of plant species that were able to coexist in experimental old-field plots dominated by *Schizachyrium scoparium*. Despite the evidence building from such experimental studies and theoretical discussion, it has yet to be confirmed that the principles of limiting similarity (Pacala and Tilman 1994) can be successfully used to exclude a target invasive plant species in the context of an operational prairie restoration.

Planting may occur during the dormant season or the growing season and may involve broadcasting or drilling seeds. The effect these methods might have on Canada thistle growth from an existing propagule bank is not clear. For example, soil disturbance caused by a seed drill might bring more propagules to the surface where they could establish, or broadcast seed might be vulnerable to predators or desiccation (Howe and Brown 1999), leaving more resources available for invasives (Davis et al. 2000). Dormant-season seeding might allow planted species to establish earlier and become competitive with thistle (Körner et al. 2008), or the herbicide typically applied before planting in the growing season might be more effective at reducing competitiveness of thistle.

Our goal in this study is to assess the roles of planted species richness and limiting similarity on invasion by Canada thistle in realistic prairie restoration settings, which we hope will inform and improve the practice of tallgrass prairie restoration. In this context, if increasing the species richness of the seed mix while maintaining a constant number of seeds reduces invasibility, cover of Canada thistle should decline as seed mix species richness increases. Likewise, if limiting similarity reduces invasion of Canada thistle, we expect to see stronger negative effects of perennial forbs, and especially those in the Asteraceae, than of other guilds on cover of Canada thistle. Lag effects (effects of cover of a guild measured in year x on Canada thistle in years $x + 1$ or $x + 2$) should become increasingly negative as declining space, light, and nutrients increase the likelihood of biotic interactions: functionally similar species may co-occur at the beginning of a restoration due to common habitat requirements, but competition may not be evident until some shared resource becomes limiting. We used structural equation models (SEM; Grace 2006) to assess the impact of cover of planted and non-planted guilds (as defined by Brown (2004), with perennial forbs divided between those in the Asteraceae and others) on cover of Canada thistle (Fig. 1; see "Methods" for details of analysis).

Methods

Study sites

The study was conducted on fields formerly in a corn-soybean cropping rotation on US Fish and Wildlife

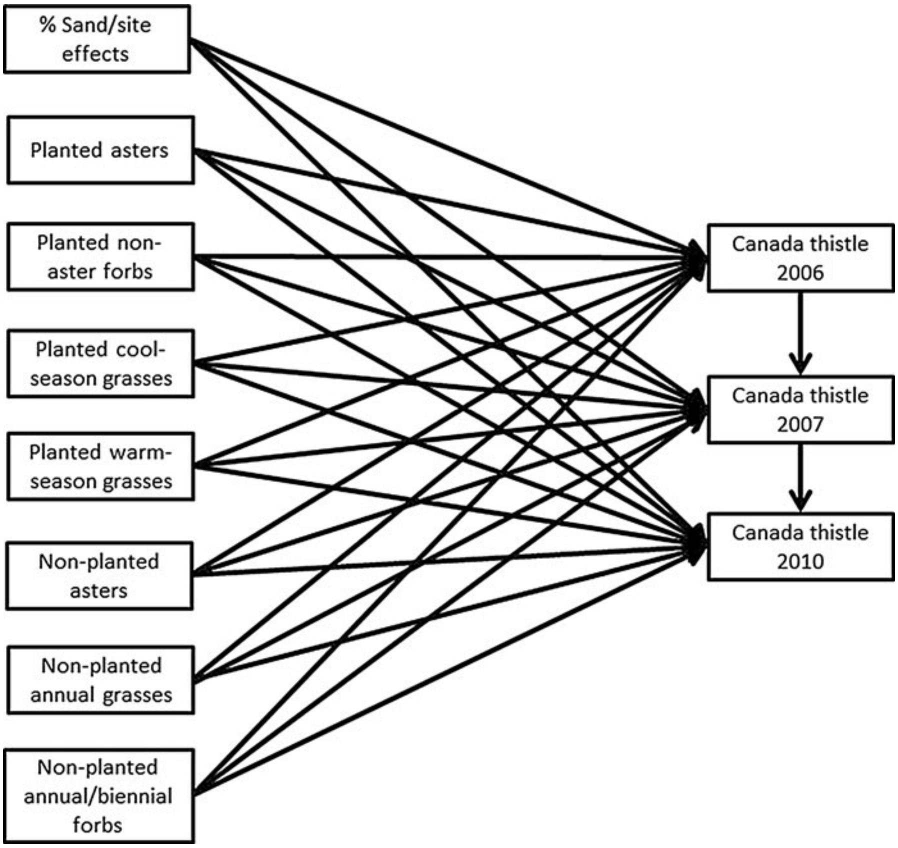

Fig. 1 Initial structural equation model describing potential relationships between cover of planted and non-planted guilds measured in 2006 and cover of Canada thistle in 2006, 2007 and 2010. Percent sand/site effects is a variable to account for differences among the six fields. All independent variables are correlated with one another. All variables, except % Sand/site effects, were transformed ($\ln(y + 1)$). Models for effects of guilds measured in 2007 on Canada thistle in 2007 and 2010 and for effects of guilds measured in 2010 on Canada thistle in 2010 were similar, except that some independent variables dropped out and some were added, based on sufficient abundance (see Fig. 3)

Service property at Fergus Falls, Morris, and Litchfield Wetland Management Districts (WMDs), Minnesota, USA. Treatments (see below) were applied to two fields at each of the three WMDs, for a total of six experimental fields (sites) representing a range of soil types and textures (Table 1). Total area treated in each field was about 1.62 hectares (4 acres). The treatment area was divided into 108 cells, each 12.2 × 12.2 m (0.015 ha). Sampling (see below) was restricted to a 2 × 6 m plot in the center of the treated cell to minimize edge effects. A buffer zone, planted to native grasses and equivalent to the width of a cell, separated rows of cells to accommodate equipment and plot access. Treatments were assigned to cells at random with 12 replications per treatment in each field. Growing-season precipitation (May–September) was variable, but generally below the long-term average throughout much of the study, except in 2005 and 2010 (http://www.hprcc.unl.edu/data/historical; Fig. 2). The Canada thistle propagule bank at these sites prior to restoration was very limited, ranging from a high of nine plots with ≥1 seed at the Heinola site (Fergus Falls WMD) to zero at the Meeker site (Litchfield WMD); no vegetative propagules sprouted (Larson 2009). Nonetheless, an average of 26 plots per site (range 9–50) were infested with Canada thistle in the 2005 growing season and 52.5 (range 19–88) in 2006.

Treatments

The three planting methods were a dormant-season broadcast seed application, applied when ground was frozen [December 2004–March 2005, hereafter dormant broadcast (DB)]; a growing-season broadcast seed application; and a growing-season seed drilling application. Growing-season treatments were applied as soon as equipment could enter the fields [due to wet conditions, June–July 2005; for simplicity, we will refer to these treatments as summer broadcast (SB) and summer drill (SD)]. Continued wet weather after treatment in 2005 minimized the potential water stress that might be expected of such a late planting.

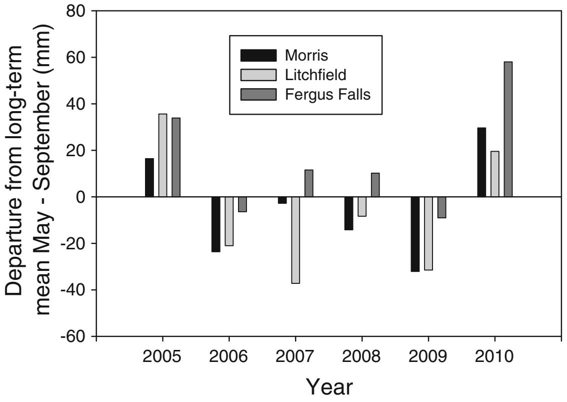

Fig. 2 Departures from mean growing-season precipitation, 2005–2010 near study fields in Morris, Litchfield, and Fergus Falls Wetland Management Districts

Seed mixtures included low-, medium-, and high-richness mixes of 10, 20 and 34 species, respectively. Proportion of seeds in each guild [cool-season grasses (20 % by number), warm-season grasses (50 %), legumes (10 %) and non-leguminous perennial forbs (hereafter perennial forbs; 20 %)], were maintained regardless of seed species richness. Within perennial forbs, 75 % were in the Asteraceae in each seed mix. All the species in the low richness mix were included in the medium richness mix and all the species in the medium richness mix were included in the high richness mix (Table 2), thus we cannot test effects of diversity independent of species composition. Seed was produced within the prairie ecoregion of the upper Midwest, was purchased from the nearest available

Table 1 Soil associations and mean soil texture of study fields (Fergus Falls, Litchfield, and Morris Wetland Management Districts); Shown are means ± their standard errors for soil texture measures (Larson 2009)

Station	Field	Soil association	Clay (%)	Sand (%)	Silt (%)
Fergus Falls	Heinola	Kandota-Knute-Brandsvold	8.05 ± 0.25	71.99 ± 0.78	19.96 ± 0.64
	Meadows	Hamerly-Doran	16.13 ± 0.37	71.40 ± 0.45	12.48 ± 0.21
Litchfield	Kandiyohi	Canisteo-Nicollet	20.32 ± 0.41	55.58 ± 0.76	24.10 ± 0.50
	Meeker	Fieldon-Litchfield-Dasson	7.09 ± 0.25	82.42 ± 0.91	10.49 ± 0.71
Morris	Diekmann	Aazdahl-Hamerly-Lindaas	24.33 ± 0.48	53.66 ± 0.44	22.01 ± 0.24
	Fahl	Barnes-Buse-Svea	14.41 ± 0.22	64.18 ± 0.62	21.41 ± 0.45

Table 2 Species composition of functional groups in the seed mixes at Minnesota WMDs; nomenclature follows USDA Plants (plants.usda.gov), accessed Jan. 7, 2011

Seed mix richness	Guild	Species
Low–medium–high	Warm-season grass	*Andropogon gerardii* Vitman[a]
	Warm-season grass	*Bouteloua curtipendula* (Michx.) Torr.[b]
	Legume	*Dalea purpurea* Vent.
	Cool-season grass	*Elymus canadensis* L.[c]
	Asteraceae	*Helianthus maximiliani* Schrad.
	Perennial forb	*Monarda fistulosa* L.
	Warm-season grass	*Schizachyrium scoparium* (Michx.) Nash
	Warm-season grass	*Sorghastrum nutans* (L.) Nash
	Asteraceae	*Symphyotrichum novae-angliae* (L.) G.L. Nesom
	Perennial forb	*Verbena stricta* Vent.
Medium–high	Asteraceae	*Artemisia ludoviciana* Nutt.
	Asteraceae	*Coreopsis palmata* Nutt.
	Legume	*Dalea candida* Michx. ex Willd.
	Asteraceae	*Heliopsis helianthoides* (L.) Sweet
	Legume	*Lespedeza capitata* Michx.
	Warm-season grass	*Panicum virgatum* L.[d]
	Perennial forb	*Potentilla arguta* Pursh
	Asteraceae	*Oligoneuron rigidum* (L.) Small
	Warm-season grass	*Sporobolus compositus* (Poir.) Merr.
	Perennial forb	*Zizia aurea* (L.) W.D.J. Koch
High	Perennial forb	*Allium stellatum* Fraser ex Ker Gawl.
	Perennial forb	*Asclepias verticillata* L.
	Sedge	*Carex vulpinoidea* Michx.
	Legume	*Desmodium canadense* (L.) DC.
	Asteraceae	*Echinacea angustifolia* DC.
	Cool-season grass	*Elymus trachycaulus* (Link) Gould ex Shinners[e]
	Asteraceae	*Liatris aspera* Michx.
	Asteraceae	*Ratibida columnifera* (Nutt.) Woot. & Standl.
	Asteraceae	*Rudbeckia hirta* L.
	Asteraceae	*Solidago speciosa* Nutt.
	Cool-season grass	*Nassella viridula* (Trin.) Barkworth[f]
	Asteraceae	*Symphyotrichum laeve* (L.) A. Löve & D. Löve
	Perennial forb	*Vernonia fasciculata* Michx.

Cultivars: [a] Bison Big Bluestem, [b] Pierre Sideoats Grama, [c] Mandan Canada Wildrye, [d] Dacotah Switchgrass, [e] Revenue Slender Wheatgrass, [f] Lodorm Green Needle

supplier, and included cultivars of a few grass species (Table 2); seed was purchased from the same suppliers, mixed, and planted with the same equipment on all study fields. We planted approximately 430 seeds/m^2, regardless of richness of the mix. The seed drill was designed to plant seeds at a depth of 0.635 cm (0.25 in), with a range of 0–1.27 cm (0–0.5 in). All fields were mowed (residue was not removed) once in each of the first 2 years in early summer to reduce competition for light and water from annual weeds, per standard restoration practice. We applied glyphosate to the SB and SD cells prior to seeding. Soybean meal was used as a carrier in the broadcast seedings and vermiculite was used in the drilled seedings. A cultipacker was used to ensure good seed-to-soil contact after summer broadcast seeding. The fields were burned in spring 2009.

A 0.25 m × 4 m subplot was randomly placed and permanently marked within the 2 m × 6 m plots described above; here we visually estimated aerial cover of each species (total cover could therefore exceed 100 %) once in mid-June through August

2006, 2007, and 2010. Species richness was evaluated by counting all species encountered in the 2 m × 6 m plot in 2007 and 2010. The richness data were used to test the efficacy of the seed mix species richness; planted species richness was found to increase significantly with seed mix richness (Larson et al. 2011). Field work began at Litchfield WMD and progressed northward to maintain a phenologically consistent sample across the six fields.

Statistical analysis

We used mixed models [Proc Mixed in SAS version 9.2 (SAS Institute Inc. 2008)] in a randomized block design with repeated measures (each field was a random block, year was the repeated measure and plots were subsamples nested within each field, planting method, and seed mix richness) to evaluate the role of seed mix richness, planting method, and their interaction on proportion of total live cover comprising Canada thistle. Significance was set at $P \leq 0.05$. We found no evidence that seed mix richness influenced Canada thistle cover (see "Results"), so SEMs focused on effect of guilds on Canada thistle cover taking only planting method into account.

We used SEMs in a multigroup analysis (Grace 2003, 2006) in IBM SPSS Amos, version 19 (Amos Development Corporation, Meadville, PA), to evaluate the effects of cover of different species guilds on Canada thistle cover in 2006, 2007 and 2010 under the three planting methods. The multi-group analysis allowed us to assess whether or not the data from each planting method were consistent with a single model. Using the procedures described by Grace (2006, page 184), we first assessed fit to a single model form. If model form was consistent among planting methods, we then assessed consistency of the path coefficients. If path coefficients from predictor variables (guilds) to Canada thistle were found to vary among the three planting methods, a separate model was developed for each planting method since the goal was to understand relative effects of the predictor variables; by developing independent models, we could remove nonsignificant paths, which resulted in better estimates of the remaining path coefficients. If path coefficients were found not to vary among planting methods, we further tested for consistency among intercepts, means, covariances and residuals, consecutively, progressing only if the previous level was consistent among groups. Species were separated into planted guilds: (1) warm-season grasses (2) cool-season grasses (3) perennial Asteraceae forbs, and (4) perennial non-Asteraceae forbs; and non-planted guilds: (5) annual/biennial forbs (2006 and 2007) (6) legumes (2007 and 2010) (7) perennial Asteraceae forbs (8) annual grasses (2006), and (9) cool-season grasses (2007 and 2010). Percent cover of each guild each year is presented as a point of reference to aid in interpreting the results (Fig. 3). By 2010, non-planted annual/biennial forbs had declined to a point that they could no longer be statistically analyzed; by 2007 non-planted cool-season grasses and legumes had increased and could be included in the analysis. Non-planted non-Asteraceae forbs were never abundant enough to include in statistical analyses. Planted legume establishment was too low and irregular for statistical analysis and sedges also were sparse, irregularly encountered, and presented identification problems, so are not included. Models were analyzed separately for effects of cover of guilds in 2006 on Canada thistle in 2006, 2007 and 2010; cover of guilds in 2007 on Canada thistle in 2007 and 2010; and cover of guilds in 2010 on Canada thistle in 2010.

Our approach was model-generating, rather than strictly confirmatory (Jöreskog and Sörbom 1996); although we could hypothesize that some guilds, e.g. perennial Asteraceae, would be more likely to limit the establishment or spread of Canada thistle, the uncertainty associated with colonization of plots devoid of plants at the beginning of the study and the likelihood that conditions would change over time, lead us to a greater interest in relative effects of the various guilds than to confirmation of a particular hypothesis. We thus began with all candidate guilds as described above in each model, assessing fit, then trimming guilds with clearly non-significant pathways ($P > 0.15$), contingent on minimal reduction in R^2 associated with the response variables. All of the model variables were measured in the field, and thus are manifest variables. Variables were assessed for outliers (none were found) and general distribution using scatter plots (see Online Resource 1) and for multivariate kurtosis using metrics calculated within Amos; all cover variables except cover of cool-season grasses in 2007 were transformed ($\ln(y + 1)$) to reduce multivariate kurtosis and improve normality. Natural log-transformation is not typical for data expressed in proportions, but the abundance of zeroes in our data made this the only acceptable transformation

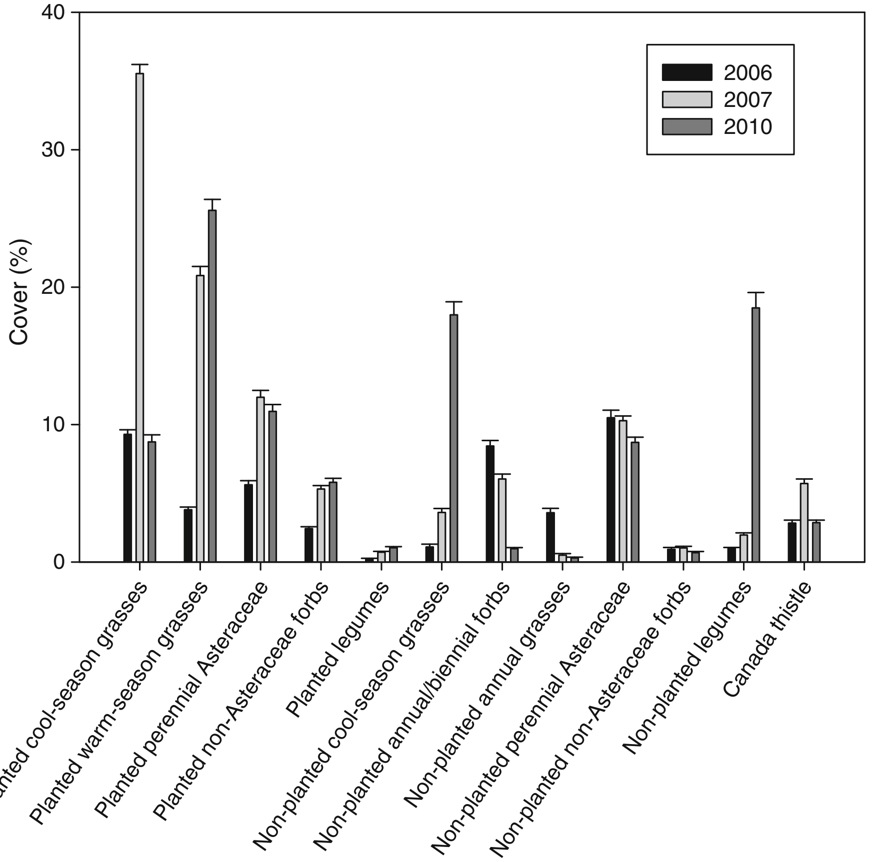

Fig. 3 Mean percent cover of planted and non-planted guilds and Canada thistle across six study fields in 2006, 2007, and 2010

for most variables. An additional advantage to ln-transformation of both dependent and independent variables is that raw path coefficients can be interpreted as expected proportional change in the response variable per proportional change in the predictor variable (Gelman and Hill 2007, p. 64).

To account for site-level variation, a nonmetric multidimentional scaling analysis was conducted in PC-Ord version 5.2 (McCune and Mefford 2006). In this analysis, variables for soil texture and nitrogen dynamics (mineralization and nitrification) on plots were used in the main matrix and sites were entered in the second matrix. The resulting dominant synthetic axis accounted for 74 % of the variation in the data and was highly correlated ($r = 0.99$) with percent sand (data not shown), so percent sand was used as a covariate in the SEMs to account for site effects. Soil texture was measured on only one-third of the plots at each site (Larson et al. 2011); a kriging analysis indicated no within-site spatial structure, so missing percent sand values were imputed within sites using regression imputation as implemented in AMOS version 19 (Arbuckle 2010). Cover measurements of all guilds in 2006 were used as predictors in the regression. Within the SEM, sand/site effects were modeled as direct effects on the response variables and as correlations with predictor variables, which themselves were all inter-correlated. Percent sand/site effects were not ln-transformed so the raw path coefficients are not comparable to those of the guilds. We calculated standardized path coefficients to facilitate comparisons, but caution that standard deviations in soil texture are not necessarily equivalent to standard deviations in plant cover (Grace and Bollen 2005). Model coefficients of determination were calculated with and without guilds to assess how much variation the guilds accounted for in excess of simple sand/site effects.

Results

Planting method and seed mix richness

Seed mix richness had no effect on proportion of live cover comprising Canada thistle (Table 3). No interaction was detected between planting method and seed mix richness. Even though the DB method had greater Canada thistle cover in 2006 and 2007, by 2010 methods did not vary in this respect (data not shown).

Limiting similarity

Although the hypothesized model form fit all three planting methods ($X^2 = 0.768$, df = 3, $P = 0.857$), path coefficients for effects of cover of guilds in 2006 on cover of Canada thistle in 2006, 2007, and 2010 varied significantly among planting methods ($X^2 = 110.13$, df = 55, $P > 0.001$), so each method was modeled separately (Fig. 4, Online Resource 2). Planted perennial Asteraceae never had a negative effect on Canada thistle in any of the 2006 models, but in SB (Fig. 4b) and SD (Fig. 4c) plots there was a positive association within 2006 and in SD a small positive lag effect for Canada thistle in 2010. Non-planted Asteraceae had significant effects on Canada thistle only in the DB (Fig. 4a) plots, with a small positive association in 2006 but a negative lag effect of similar magnitude in 2010. Although there was no significant effect of non-planted Asteraceae in 2006 in SB plots, there was a negative lag effect in 2007. Among the planted species assessed in 2006, non-Asteraceae forbs and cool-season grasses were most commonly negatively associated with Canada thistle in 2006 and 2007. Although non-planted annual/biennial forbs had a positive association with Canada thistle in 2006 in SD plots, lag effects on Canada thistle in 2010 SB and SD plots were negative. Non-planted annual grasses had a relatively strong negative effect in DB plots in 2006, but lag effects in 2007 were positive; annual grasses had positive associations with Canada thistle in SB plots and were never a significant factor in SD plots. Canada thistle had significant positive effects on its own cover between sample years.

We could not assess the unconstrained model form for effects of guilds on Canada thistle cover in 2007 and 2010 because there were no degrees of freedom associated with the full model. Path coefficients varied significantly among planting methods ($X^2 = 64.28$, df = 38, $P = 0.005$), so methods were modeled separately (Fig. 5, Online Resource 3). Planted Asteraceae were again either not associated with Canada thistle cover, or (in three cases, only one of which was significant) the association was positive (Fig. 5). In contrast, planted cool-season grasses, which reached their peak cover in 2007 (Fig. 3), had significant negative effects on Canada thistle cover in all three planting methods within 2007, although there was a positive lag effect on DB plots in 2010. Planted warm-season grasses also were beginning to exhibit negative effects on Canada thistle in 2007, with significant negative lag effects in 2010 in SB and SD plots. Planted non-Asteraceae forbs had a small, but significant, negative effect on Canada thistle in 2007 SB plots. With the exception of non-planted Asteraceae in DB plots, all non-planted guilds had negative effects on Canada thistle, the strongest of which was for legumes in SD plots. As in the 2006 model, the effect of Canada thistle on itself in the subsequent sample year was significant and positive.

By 2010, path coefficients and intercepts did not vary among planting methods in the model with

Table 3 Mixed model results for effects of seed mix richness, planting diversity, year, and their interactions on Canada thistle [transformed, ln(y + 1)]

Effect	Numerator DF	Denominator DF	F value	*P*
Year	2	90	23.67	<0.0001
Planting method	2	40	4.47	0.0177
Seed mix richness	2	40	0.05	0.9517
Year × method	4	90	4.54	0.0022
Year × richness	4	90	0.41	0.8009
Method × richness	4	40	1.31	0.2844
Year × method × richness	8	90	0.03	1

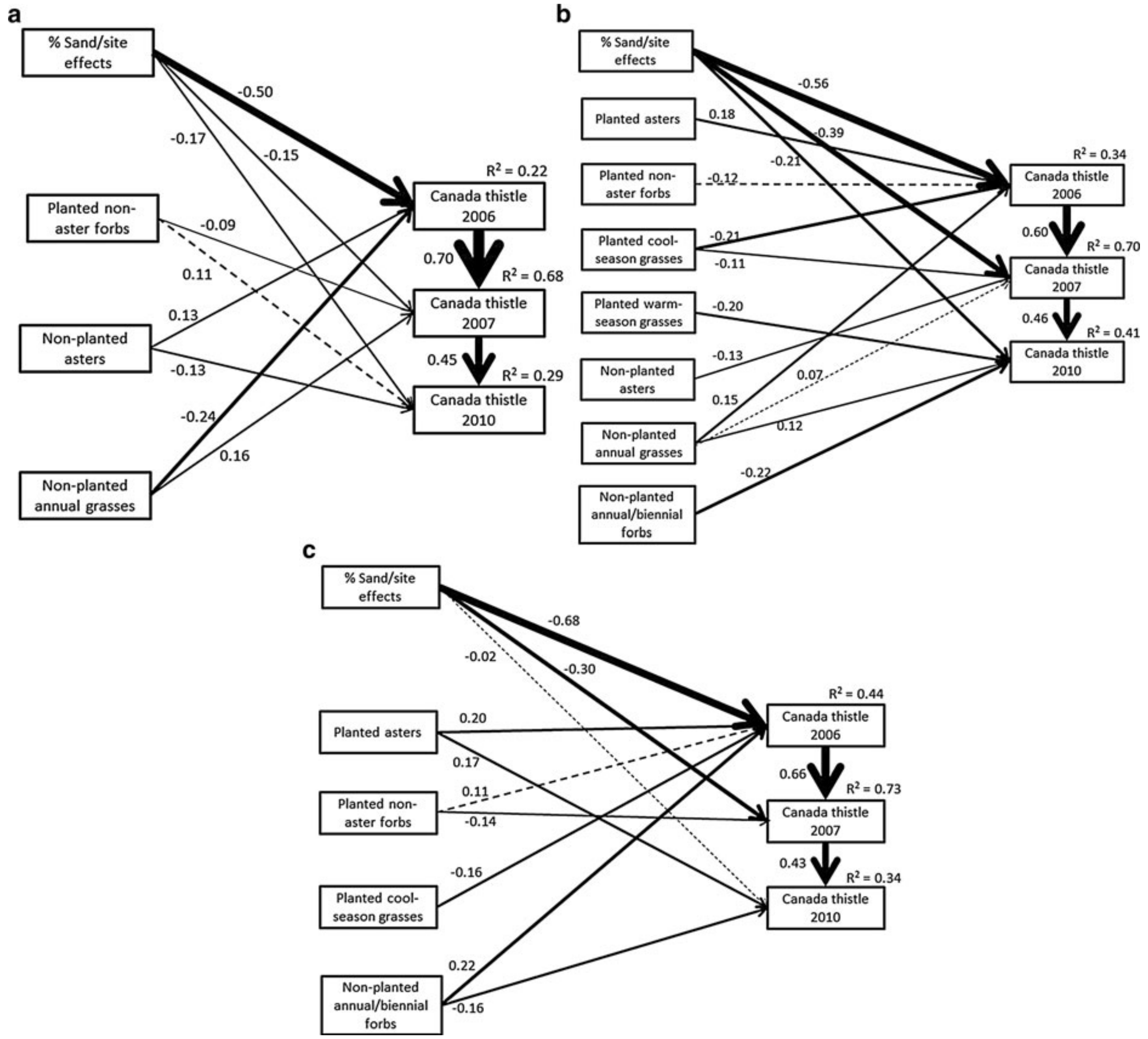

Fig. 4 Results of structural equation models for effects of cover of guilds measured in 2006 on cover of Canada thistle measured in 2006, 2007, and 2010 in (**a**) Dormant Broadcast (**b**) Summer Broadcast, and (**c**) Summer Drill plots. Thickness of each arrow is proportional to its standardized path coefficient, which is displayed next to each arrow. Marginally non-significant paths are depicted with dashed arrows. Non standardized path coefficients and P-values can be found in Online Resource 2

nonsignificant paths removed ($X^2 = 14.25$, df = 10, $P = 0.162$), but structural means did ($X^2 = 91.56$, df = 18, $P < 0.001$). All significant effects on Canada thistle, except those of planted cool-season grasses, were negative (Fig. 6, Online Resource 4). Neither planted nor non-planted Asteraceae, nor indeed any forb guild, had a significant effect on Canada thistle in 2010. The strongest effect was that of non-planted legumes.

In all cases, most of the variance in cover of Canada thistle in the SEMs could be accounted for with sand/site alone (Table 4). Guilds accounted for a relatively larger proportion of variance within-year in DB than in SB or SD plots in 2007 and 2010; guilds never accounted for more variance in SD than in DB or SB plots except in the 2006 model for 2010 Canada thistle cover (17 % in SD versus 14 % in SB and 8 % in DB; Table 4).

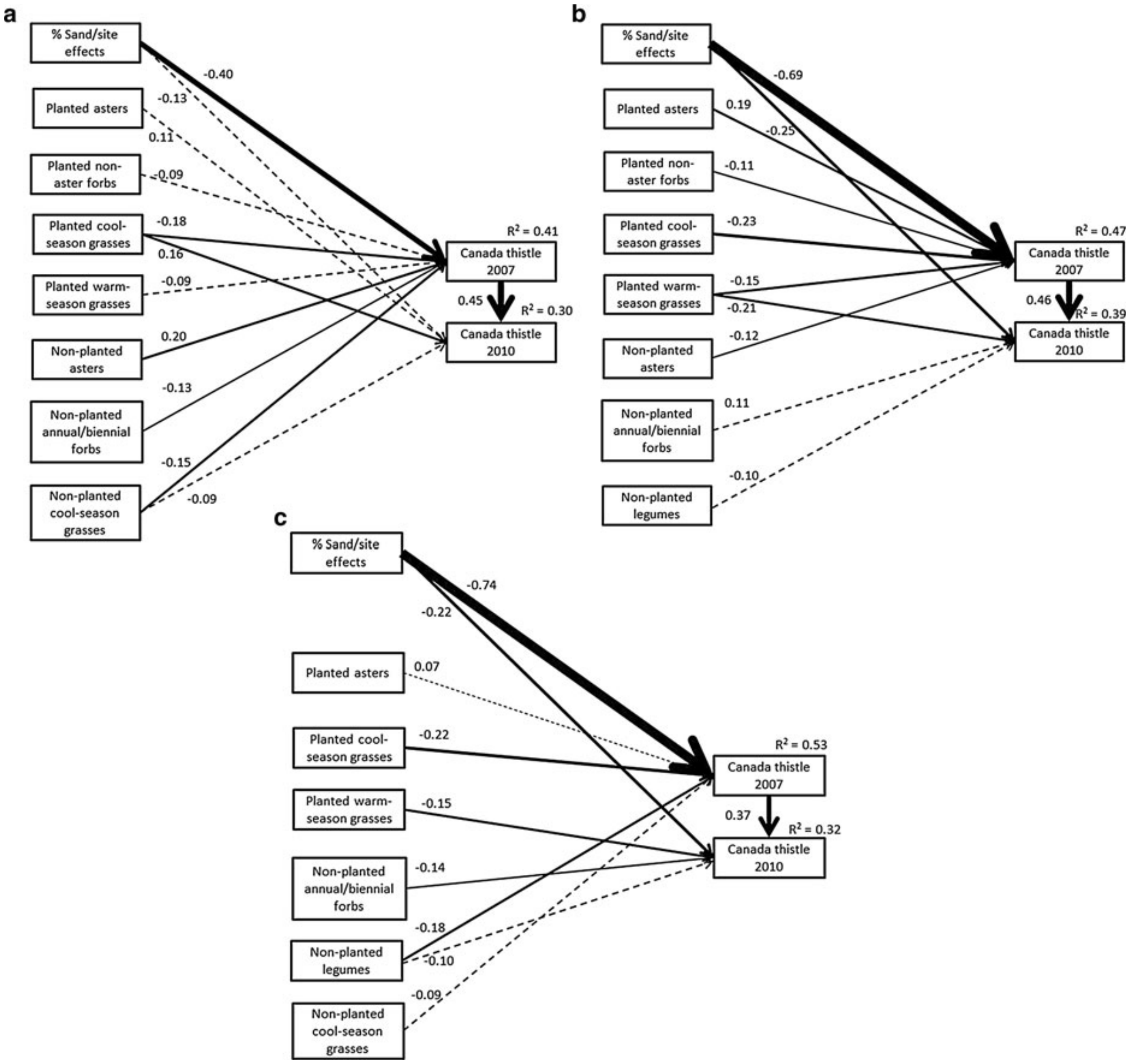

Fig. 5 Results of structural equation models for effects of cover of guilds measured in 2007 on cover of Canada thistle measured in 2007 and 2010 in (**a**) Dormant Broadcast (**b**) Summer Broadcast, and (**c**) Summer Drill plots. Thickness of each arrow is proportional to its standardized path coefficient, which is displayed next to each arrow. Marginally non-significant paths are depicted with dashed arrows. Nonstandardized path coefficients and P-values can be found in Online Resource 3

Discussion

Seed mix richness

We found no advantage (or disadvantage) in increasing the number of species planted while maintaining the same total number of seeds. These results are consistent with those of Lavorel et al. (1999), who found that richness of species within functional groups had no effect on success of experimental introduction of either of two invasive *Conyza* species in a Mediterranean system. In their study, as in ours, the native plant community was developed from seed, although they introduced the invader as seedlings in the second year of the study and evaluated growth and survival, while the invader in our study emerged from the propagule bank or via natural dispersal.

Lepš et al. (2007) found that 8 years after planting in ex-arable fields across Europe, plots that received either a low diversity (4 spp.) or a high diversity (15

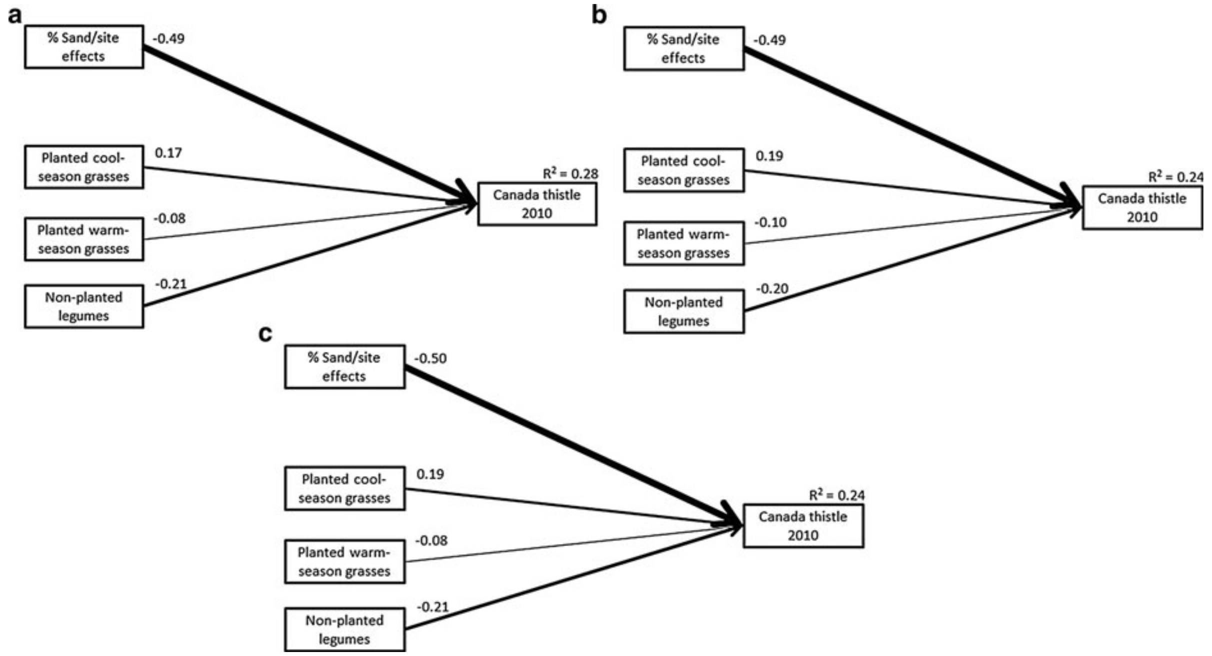

Fig. 6 Results of structural equation models for effects of cover of guilds measured in 2010 on cover of Canada thistle measured in 2010 in (**a**) Dormant Broadcast (**b**) Summer Broadcast, and (**c**) Summer Drill plots. Thickness of each arrow is proportional to its standardized path coefficient, which is displayed next to each arrow. Nonstandardized path coefficients and P-values can be found in Online Resource 4

spp.) seed mix had lower species richness and higher productivity than plots that had not been seeded but had been colonized naturally, suggesting that the planted species reduced colonization. Earlier in the experiment, plots planted to the higher diversity mix also had less colonization than those planted to the lower diversity mix, although the effect disappeared over time; the authors speculated that greater diversity provided more functional redundancy, such that if one species failed to thrive, a similar species would be present to take its place. In as much as we did not have a non-planted treatment, our results are consistent with the eighth-year results reported by Lepš et al. (2007), but it is important to note that their seeding rate was substantially higher than ours (3,500/m^2 versus 430/m^2, respectively). We lack an estimate of the number of seeds in the seed bank, however, and some of these species had negative effects on cover of Canada thistle, so our "effective" seeding rate is unknown. In any event, the existing seed bank is largely outside the control of the practitioner.

Negative effects of species richness on invasibility have typically been documented for resident richness levels below 10 (e.g., Knops et al. 1999; Naeem et al. 2000), which was our lowest species richness. We therefore may have had little opportunity to observe such effects. Nonetheless, our richness levels were typical of operational restorations and therefore reflect the likely experience of practitioners. Studies on effects of species richness on invasion also have more typically examined invasion into mature vegetation (e.g., Dukes 2001; Roscher et al. 2009; Tilman 1997). It may be unrealistic to expect that newly establishing species would have a similar effect on an invasive establishing at essentially the same time. We note, however, that measured richness of planted species in our plots in 2007 and 2010 was uncorrelated with Canada thistle stem counts in those years (data not shown), which suggests that even as planted species became established, increased richness did not reduce spread of Canada thistle.

Limiting similarity

We found no evidence that planted perennial Asteraceae could limit invasion by Canada thistle at our

Table 4 Variance in Canada thistle cover accounted for in each SEM reported in Figs. 4, 5, and 6

Years	Planting method[a]	Response variable	Full[b]	Pared[c]	Sand/site[d]	Proportion guilds[e]
2006	DB	Canada thistle (2006)	0.234	0.224	0.172	0.232
		Canada thistle (2007)	0.680	0.675	0.647	0.041
		Canada thistle (2010)	0.301	0.288	0.265	0.080
	SB	Canada thistle (2006)	0.343	0.340	0.255	0.250
		Canada thistle (2007)	0.696	0.695	0.673	0.032
		Canada thistle (2010)	0.428	0.413	0.353	0.145
	SD	Canada thistle (2006)	0.441	0.441	0.371	0.159
		Canada thistle (2007)	0.735	0.728	0.711	0.023
		Canada thistle (2010)	0.353	0.344	0.284	0.174
2007	DB	Canada thistle (2007)	0.407	0.407	0.282	0.307
		Canada thistle (2010)	0.313	0.303	0.265	0.125
	SB	Canada thistle (2007)	0.479	0.466	0.375	0.195
		Canada thistle (2010)	0.396	0.394	0.353	0.104
	SD	Canada thistle (2007)	0.538	0.533	0.448	0.159
		Canada thistle (2010)	0.339	0.324	0.284	0.123
2010	DB	Canada thistle (2010)	0.273	0.279	0.174	0.376
	SB	Canada thistle (2010)	0.246	0.240	0.174	0.275
	SD	Canada thistle (2010)	0.258	0.241	0.174	0.278

[a] *DB* dormant broadcast, *SB* summer broadcast, *SD* summer drill

[b] R^2 for the model with all possible plant guilds included

[c] R^2 for the model with only significant or near significant paths (see methods)

[d] R^2 for the model with only Sand/site effects

[e] Proportion of variance explained by guilds in the pared model [1-(variance accounted for by sand effects/total variance accounted for by pared model)]

tallgrass prairie restoration sites: there were no negative effects of planted Asteraceae in any model. On the other hand, non-planted annual/biennial (which included both Asteraceae and other families) and perennial Asteraceae present in the seed bank did have negative effects on Canada thistle cover, especially in the first 2 years after the restoration was planted. Of particular interest, direct effects of the non-planted annual/biennial cover in 2006 and 2007 persisted to 2010 in SB and SD plots, and effects of non-planted perennial Asteraceae in 2007 persisted to 2010 in DB plots. These lag effects must be mediated by something other than competition for space and/or light. By far the most common of the non-planted ruderal natives through 2007 were horseweed (*Conyza canadensis* (L.) Cronquist), annual ragweed [*Ambrosia artemisiifolia* (L.)], and Canada goldenrod [*Solidago canadensis* (L.)]. Each of these is a serious invader worldwide (Bassett and Crompton 1975; Weaver 2001; Werner et al. 1980) and has been implicated in allelopathy and effects on soil biota (Bassett and Crompton 1975; Jin et al. 2004; Kardol et al. 2007; Pisula and Meiners 2010; Werner et al. 1980; Zhang et al. 2009, 2010), suggesting that effects may persist even as the species decline. Perry et al. (2009), using activated carbon treatments in a greenhouse experiment, observed that annual ragweed was the only species studied to have allelopathic effects on Canada thistle. Perry et al. (2009) pointed out that to be effective, a cover crop must disadvantage invasive species more than the desired species. If allelopathic root exudates of an invasive plant are more toxic to its “new” than its “old” neighbors (Hierro and Callaway 2003), the converse should also be true when the resident ruderals themselves produce exudates, the invasive (in our case Canada thistle) is the “new” neighbor, and the planted species are the “old” neighbors that have adapted to the exudates.

In contrast to the annual and biennial forbs, non-planted annual grasses never had negative effects beyond the year in which they were measured, but invariably had positive lag effects. This pattern suggests that death of annual grasses may have left open spaces available for colonization by Canada thistle in subsequent years. Planted warm-season grasses measured in 2006, on the other hand, had only lag effects on Canada thistle cover, suggesting that their effects increased as they grew. By 2007 and 2010, planted warm-season grasses were beginning to have within-year negative effects on Canada thistle. Planted cool-season grasses demonstrate yet a third pattern; within-year effects were negative in 2006 and 2007, but positive in 2010. In this case, it seems likely that the prescribed fire applied in spring 2009 weakened the planted cool-season grasses, allowing expansion of Canada thistle into areas previously occupied by the grasses. Spring burns have been shown to reduce abundance of cool-season species in tallgrass prairie (Howe 1995). The 2009 prescribed fire also is likely responsible for the increase in cover of non-planted legumes (DiTomaso et al. 2006) which had negative effects on Canada thistle in 2010.

Together, these results suggest a relatively limited role for functional similarity in resistance of new (i.e., within the first 5 years of planting) prairie restorations to invasion by Canada thistle. Although non-planted forbs did have negative effects on cover of Canada thistle, the effects are at least as likely due to characteristics of the particular species that established from the seed bank as to similarities in resource use, especially since the forbs deliberately planted, though abundant (Fig. 3) had little effect. Moreover, the presence of species in the existing seed bank is a matter of chance outside the control of the restoration practitioner; planting agricultural weeds such as horseweed and ragweed, despite their potential utility in restoration establishment, might be a difficult step to take under most circumstances.

Site-related factors

Despite the effects attributed to various guilds, the fact remains that most of the variance in cover of Canada thistle was related to site-specific causes that did not include vegetation characteristics we measured. Soil texture was certainly a part of this—percent sand was always negatively related to cover of Canada thistle—but because percent sand also represented unmeasured aspects of site, our analysis has limited power to distinguish specifically how the variable sand/site affected Canada thistle. Nordmeyer and Hausler (2004) did not find a significant correlation between distribution of Canada thistle and soil sand content across a single agricultural field in Germany. Tiley (2010), citing studies done in Ohio, USA, reported that vegetative spread of Canada thistle was greatest in clay and least in sand, but this may be modified by moisture availability, which also varied among sites in the present study.

Implications for restoration practice

Even though the hypothesized benefit of increasing planted species richness did not materialize, it was encouraging to observe no detrimental effect, either. Reducing propagule pressure of an influential species could have made the higher-richness plots more vulnerable to invasion by Canada thistle, but this did not happen within the seed densities in our study. Species richness was still increasing on these study sites as of 2010 (Larson et al. 2011), so it is yet unclear if greater expression of the planted seed richness will eventually forestall invasion by Canada thistle.

Although guild-level similarity between planted species and Canada thistle did not have the anticipated negative effect on cover of Canada thistle, our results do suggest a way forward. First, early, robust establishment of ruderal species, be they planted (cool-season grasses) or not (annual/biennial and perennial forbs from the seed bank), were effective at limiting increases in cover of Canada thistle. Even though cool-season grasses may lack persistence in tallgrass prairies (Liegel and Lyon 1986), they establish more quickly than warm-season grasses and may offer protection from invasion during the critical establishment phase of the later successional species. The decline of cool-season grasses we saw in 2010 was likely due, at least in part, to a dormant-season prescribed fire conducted in 2009 (Howe 1994); if one of the restoration goals is to reduce invasion of a species against which cool-season grasses are an effective deterrent, deferring burning for an extra year may be beneficial. Our restorations are still quite young and it remains to be seen if the warm-season grasses, which are just now becoming dominant, will compete effectively with the existing Canada thistle on our plots; early signs are promising, as a weak negative effect of planted warm-season grasses was seen in 2010.

Models describing effects of guilds on Canada thistle varied among planting methods in the 2006 and 2007 sample years, but not in 2010. One explanation for this pattern is that as biotic forces gain prominence in the plantings, compared with edaphic conditions that initially determine where a seed can germinate, differences among the methods decline. These restorations are only 5 years old, however, and likely have not reached an equilibrium in terms of species composition. Seed drilling has been found to favor establishment of warm-season grasses (Ambrose and Wilson 2003; Larson et al. 2011; Redmann and Qi 1992), the only planted guild to have negative effects on Canada thistle in 2010, which might lead to future reduction in Canada thistle in SD plots.

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