

RESEARCH ARTICLE

Functionally Similar Species Confer Greater Resistance to Invasion: Implications for Grassland Restoration

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Abstract

Plant community functional composition can be manipulated in restored ecosystems to reduce the establishment potential of invading species. This study was designed to compare invasion resistance among communities with species functionally similar or dissimilar to yellow starthistle (*Centaurea solstitialis*), a late-season annual. A field experiment was conducted in the Central Valley of California with six experimental plant communities that included (1) six early-season native annual forbs (AF); (2) five late-season native perennials and one summer annual forb (NP); (3) a combination of three early-season native annual forbs and three late-season native perennials (FP); (4) six early-season non-native annual grasses (AG); (5) monoculture of the late-season native perennial grass *Elymus glaucus* (EG); and (6) monoculture of the late-season native perennial *Grindelia camporum* (GC). Following establishment, *C. solstitialis* seed was added to half of the plots,

and a monoculture of *C. solstitialis* (CS) was established as a control. Over a 5-year period, the AF and AG communities were ineffective at preventing *C. solstitialis* invasion. *Centaurea solstitialis* cover remained less than 10% in the FP and NP communities, except in year 1. By the fourth year, *E. glaucus* cover was greater than 50% in NP and FP communities and had spread to all other communities (e.g., 27% cover in CS in year 5). Communities containing *E. glaucus*, which is functionally similar to *C. solstitialis*, better resisted invasion than communities lacking a functional analog. In contrast, *G. camporum*, which is also functionally similar to *C. solstitialis*, failed to survive. Consequently, species selection for restored communities must consider not only functional similarity to the invader but also establishment success, competitiveness, and survivorship.

Key words: *Centaurea solstitialis*, *Elymus glaucus*, functional similarity, *Grindelia camporum*.

Introduction

Species diversity influences many plant community properties, such as primary production, nutrient cycling, hydrodynamics, and plant community resilience and resistance (Diaz et al. 2007). Highly diverse plant communities have been hypothesized to be more stable and thus more resistant to invasion of non-native species (Elton 1958). However, empirical studies have both supported (Tilman et al. 1996) and opposed (Robinson et al. 1995) the diversity–stability hypothesis. Tilman (1997) and Symstad (2000) suggest that functional diversity is a more accurate indicator of community stability or resistance to invasion than general species diversity. Additionally, Vitousek and Hooper (1997) and Brown et al. (1998) demonstrated that communities containing species functionally similar to the

invader are more capable of resisting invasion compared to communities characterized simply by high species diversity. Functional groups are classified based on their ecological, morphological, physiological, biochemical, or life history characteristics (Lavorel et al. 2007). Thus, restored communities may better resist future invasions by incorporating species functionally similar to known high-risk invaders.

Most of the grasslands of the Central Valley of California have been invaded by non-native annual grasses. These annual grasses displaced communities of native perennial bunchgrasses and forbs beginning with the arrival of Europeans into California in the 1700s (Burcham 1956; Heady 1988). Fire suppression, agricultural disturbance, and overgrazing by cattle during periods of drought led to their dominance (Heady 1988). Once established, non-native annual grasses produce dense canopies that suppress the establishment of slower growing perennial bunchgrass seedlings (Rice et al. 1997).

More recently, many California grasslands, particularly in the Central Valley, are shifting from annual grasses to late-season deep-rooted annual forb species, particularly yellow starthistle (*Centaurea solstitialis*). This shift correlates with disturbance and canopy gaps, both of which

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increase light availability later in the growing season (Gerlach & Rice 2003). In addition, these late-season forbs utilize deep soil moisture not available to shallow-rooted annual grasses (Gerlach 2004; Young 2007).

The initial displacement of native bunchgrass communities by non-native annual grasses was not a priority to most land managers because these communities continued to produce high-value forage. However, with the spread of *C. solstitialis* into grasslands, restoration of native grassland communities has become a greater concern for public land managers and private landowners (Bugg et al. 1997).

Centaurea solstitialis is believed to have arrived in California after 1849 as a contaminant in Chilean-grown alfalfa seed (Gerlach 1997b). Following its introduction into alfalfa fields in northern California, *C. solstitialis* spread to other locations, including grain fields, via tractors, and other equipment. By 1958, *C. solstitialis* was estimated to have invaded over 250,000 ha of California, mostly in range or grasslands (DiTomaso 2000). Over the past four decades, rapid and long-range dispersal of *C. solstitialis* has occurred through extensive road building, increased suburban development, and an expansion in the ranching industry (Gerlach 1997a). The current *C. solstitialis* infestation in California has been estimated at nearly 5.7 million ha (Pitcairn et al. 2006).

Unlike native perennial bunchgrasses, *C. solstitialis* has ruderal characteristics including high seed production (Roché et al. 1994), reduced seed dormancy, and rapid root development (Sheley et al. 1993; Benefield et al. 2001). Although *C. solstitialis* is an annual forb, its morphology and phenology are different from most annual grass and broadleaf species found in California grasslands. By comparison, it appears to be functionally similar to late-season perennial grasses and forbs in its resource allocation patterns and phenology (Gerlach & Rice 2003; Gerlach 2004).

In this study, we compared resistance to *C. solstitialis* invasion in communities with species functionally similar (late season) or dissimilar (early season) to the invader or in combination (early and late season). To this end, we established communities of early-season non-native winter annual grasses, early-season native winter annual forbs, mixed late-season native perennial grasses, mixed early- and late-season native forbs and perennial grasses, and monocultures of a late-season native perennial grass and native perennial forb with and without additions of *C. solstitialis*. We hypothesized that communities with species functionally equivalent to *C. solstitialis* would better resist invasion.

Methods

Field Site

The experiment was conducted at the University of California, Davis, in the western Sacramento Valley (northern Central Valley), on a level, open field. The soil

was a coarse-loamy mixed superactive nonacidic thermic Typic Xerofluvents (Xero Fluvic Entisol). The site was previously dominated by agricultural weeds (e.g., *Bromus* spp., *Lolium* spp., *Convolvulus arvensis*, *Salsola tragus*, *Brassica* spp., *Sinapis arvensis*, and *Raphanus* spp.). There was no record of *Centaurea solstitialis* at or near the research site prior to the initiation of the experiment.

Experimental Design

All species chosen were known to occur in grassland ecosystems near the study site. The native species selected were believed to be locally prevalent prior to the invasion of non-native winter annual grasses (Burcham 1956; McNaughton 1968; Heady 1988) or *C. solstitialis* (DiTomaso 2000). For this reason, these natives are considered the most suitable for restoration programs in northern California and surrounding regions (Bugg et al. 1997). Furthermore, all native species used in this study were commercially available through a local seed producer (Hedgerow Farms, Winters, CA, U.S.A.; hedgerowfarms.com) and are known to establish well under local conditions. Therefore, native species that are functionally similar to *C. solstitialis*, like tarweeds (*Hemizonia* spp.), were not included, as they are not commercially available and are unlikely to be used in a grassland restoration. The non-native annual grasses used in this study are common components of the Central Valley grasslands in California. Seeds of these species were collected the previous season or purchased from a local company (Valley Seeds, Fresno, CA, U.S.A.).

The experimental communities comprised annual or perennial forbs and grasses, with their functional group classification based on the timing of resource use according to Hickman (1993) and DiTomaso and Healy (2007) (Table 1). Non-native winter annual grasses grow primarily during the cool, wet season (first fall rain to early April), set seed by early summer, and are shallow rooted. In general, native annual forbs are phenologically similar to the non-native annual grasses. In contrast, the native perennials reach reproductive peak during the dry summer months with their roots typically exceeding 1 m in depth (DiTomaso et al. 2003).

Elymus glaucus and the other perennial grasses are morphologically different (fibrous roots, narrow leaves) than *C. solstitialis* but functionally similar (timing of soil water use). The perennial grasses have a dense, bunched growth habit, survive moderate drought conditions, and continue to grow during the summer, given adequate soil moisture. Among them, *E. glaucus* is considered to be one of the better adapted and more robust perennial grasses native to the Sacramento Valley (Knapp and Rice 1996; Bugg et al. 1997). *Grindelia camporum*, the only perennial forb used in the study, is most closely related taxonomically, morphologically, and functionally to *C. solstitialis* of those species in this study. Both *G. camporum* and *C. solstitialis* are characterized by late-season growth and

Table 1. Species compositions in six plant communities (AG = annual grass; AF = annual forb; NP = native perennial; FP = annual forbs and perennials; EG = *Elymus glaucus*; and GC = *Grindelia camporum*).

Species	Plant Communities						Life Cycle/Plant Category	Functional similarity to <i>Centaurea solstitialis</i>
	AG	AF	NP	FP	EG	GC		
<i>Avena fatua</i>	+						ES/AG	–
<i>Aegilops triuncialis</i>	+						ES/AG	–
<i>Bromus hordeaceus</i>	+						ES/AG	–
<i>Hordeum murinum</i>	+						ES/AG	–
<i>Lolium multiflorum</i>	+						ES/AG	–
<i>Taeniatherum caput-medusae</i>	+						ES/AG	–
<i>Gilia tricolor</i>		+					ES/AF	–
<i>Lasthenia glabrata</i>		+		+			ES/AF	–
<i>Layia platyglossa</i>		+		+			ES/AF	–
<i>Lupinus bicolor</i>		+		+			ES/AF	–
<i>Nemophila menziesii</i>		+					ES/AF	–
<i>Trifolium willdenovii</i>		+					ES/AF	–
<i>Elymus glaucus</i>			+	+	+		LS/PG	+
<i>E. trachycaulus</i>			+				LS/PG	+
<i>Leymus triticoides</i>			+				LS/PG	+
<i>Nassella pulchra</i>			+	+			LS/PG	+
<i>Grindelia camporum</i>			+	+		+	LS/PF	+
<i>Lotus purshianus</i>			+				LS/AF	+
<i>Centaurea solstitialis</i>	+/-	+/-	+/-	+/-	+	+	LS/AF	+

Each species is classified into the life cycles of early season (ES) or late season (LS), and plant category including annual grasses (AG), annual forbs (AF), perennial grasses (PG), or perennial forbs (PF).

flowering, deep roots, and water use timing. Therefore, monocultures of *E. glaucus* and *G. camporum* were established in addition to mixed communities.

Communities were planted in a randomized complete block design with five replications in 4 × 4-m plots with 2-m-wide alleys between plots. Four mixed plant communities were established (Table 1): six native annual forbs (AF), five native late-season perennials plus a late-season annual (NP), three native annual and three perennial species (FP), and six non-native annual grasses (AG). The plots of each of these community types were established, with half of them seeded with *C. solstitialis* (CS) in the following fall. Monocultures of *E. glaucus* (EG) and *G. camporum* (GC) were established in five plots each, and all the plots were seeded with *C. solstitialis* the following fall.

Seeds of each community were pre-mixed, broadcast by hand, and lightly raked to incorporate them into the soil. The total seeding rate was 22.4 kg pure live seed/ha, which is within the typical range of reseeding restoration programs (J. A. Anderson, Hedgerow Farms, personal communication). Live seed weights were based on germination and purity percentages. No supplemental irrigation or nutrients were applied. All plots were planted in fall 2000 following the first rains. To ensure seed viability, seeds of each species were planted in 1-m² monoculture plots adjacent to the study site. All species in these plots germinated and established in the first season. Annual grass plots (AG) were planted in winter (January) 2002.

Seeds of *C. solstitialis* were collected locally in 2000. In fall 2001, 1 year after establishment of the native plant communities, *C. solstitialis* was broadcast seeded into the

monoculture plots and half (five replicates) the AF, NP, and FP plots (hereafter, AF + CS, NP + CS, and FP + CS, respectively), whereas the other half were not seeded. A *C. solstitialis* (CS) monoculture treatment (five replicates) also was established for comparison. Similar to AF, NP, and FP plots, half of all the non-native annual grass (AG) plots established in winter 2002 were also overseeded with *C. solstitialis* (AG + CS) in fall 2002. *Centaurea solstitialis* was overseeded at a rate of 1,000 seeds/m² (2 kg/ha), which represents about 10% of the normal seed bank in a heavily infested area. This rate was intended to simulate a 90% seed bank reduction typically achieved following a 1- to 2-year control program (DiTomaso et al. 1999). Restoration of a *C. solstitialis*-infested area usually requires 1 or 2 years of weed control to successfully establish native plant communities (DiTomaso et al. 2000).

Individual species cover measurements were taken in both spring and summer beginning in 2002 for all plots except AG. Monitoring of species in the AG plots began in summer 2003 and continued until summer 2005. Cover of all species was measured in all years and seasons except summer 2003. During this timing, cover was only recorded for *C. solstitialis* and *G. camporum*, owing to transition in project leadership. Measurements were conducted within permanent 0.5 × 0.5-m subplots in each corner of the plot (four subplots per plot), approximately 0.25 m from the plot edges. Relative species and thatch cover (and bare ground) were visually estimated to within 1% (0–10%) and thereafter to the nearest 5% (10–100% cover) for a total of 100% cover. Subplot cover values were averaged for each plot.

After 3 years of establishment without disturbance, the study site was mowed in November 2004 and 2005 to simulate fall grazing. Late-season grazing is a common practice in northern California rangelands and grassland restoration (Heady 1988).

Statistical Analysis

Total cover was analyzed by analysis of variance with the general linear model (GLM) procedure to assess the overall effect of *Centaurea solstitialis* on the experimental plant communities. Data was only collected at peak spring and summer biomass production, relating to early- and late-season functional groups. Therefore, within- and among-year covariations were minimized, precluding repeated measures analysis (Daniel 1999). Additionally, year-to-year variation prohibited statistical comparisons

across years. Pairwise contrasts of *C. solstitialis*, *E. glaucus*, and *G. camporum* between community types were conducted based on the linear combination of cover data obtained from the overall analysis (Scheiner 2001). We performed statistical analyses only on cover of *C. solstitialis* and *G. camporum* in summer 2003 because cover data for other species (e.g., *E. glaucus*) were not available. All statistical analyses were performed with SAS (2002).

Results

Annual forb cover in AF and AF + CS (prior to seeding with CS) plots was 96% in the spring after planting (2001) but declined to 13% by the fourth season after planting (data not shown). By 2005, spring flushes (<1%) of *Nemophila menziesii* and *Lasthenia glabrata* were all that remained. After 2003, native annual forbs were rarely

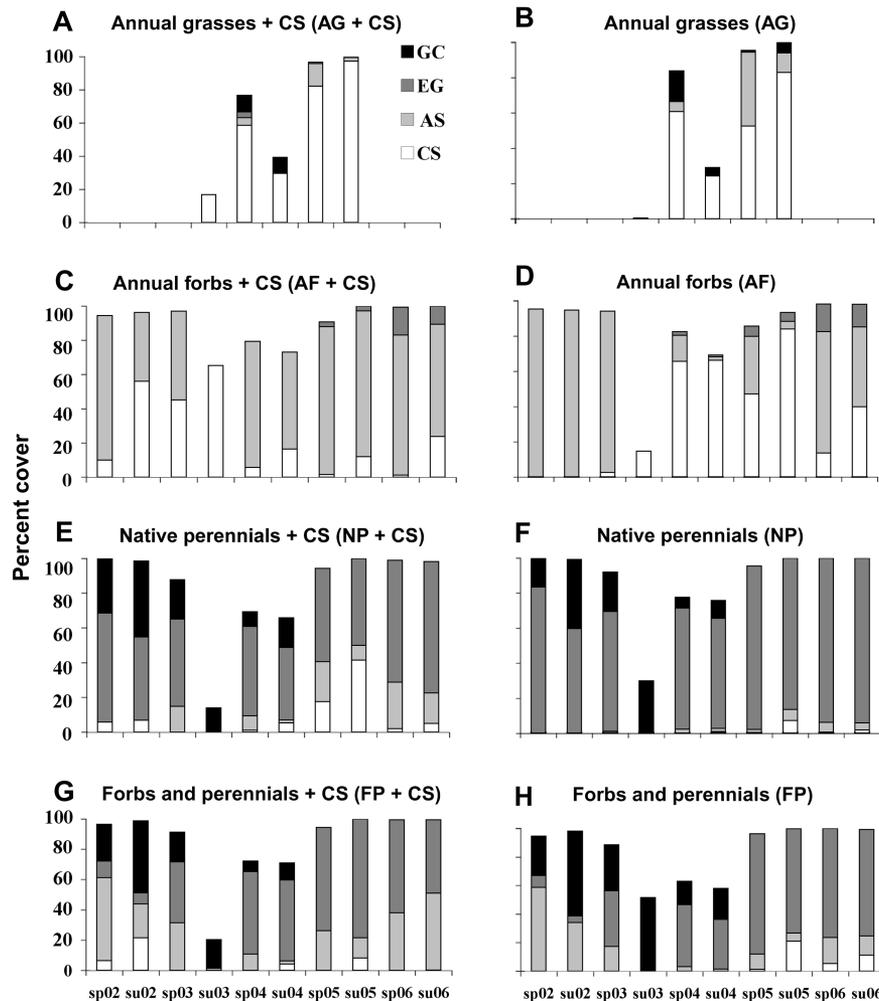


Figure 1. Percent cover from spring 2002 (sp02) through summer 2006 (su06) in (A) annual grasses with CS and (B) without CS, (C) native annual forbs with CS and (D) without CS, (E) native annual forbs and perennials with CS and (F) without CS, (G) and a mixture of native annual forbs and perennials with CS and (H) without CS showing *Grindelia camporum* (GC), *Elymus glaucus* (EG), annual species (AS), and *Centaurea solstitialis* (CS). AG and AG + CS plots were evaluated from sp04 to su05. Summer 2003 cover values only include *C. solstitialis* and *G. camporum*. Thatch and bare ground contributed to remainder of cover values not shown.

present (<1%) in AF and FP communities, and most annual species were non-native forbs and grasses (Fig. 1C–F).

By spring 2003, the native summer perennials, *E. glaucus* and *G. camporum*, dominated (>50%) all communities in which they were included (Figs. 1E–H & 2B–C). The perennials *E. trachycaulus*, *Nassella pulchra*, and *Leymus triticoides* were only rarely present (<1%) in NP and FP communities.

AG communities were dominated by *Lolium multiflorum*, which was seeded, and *Bromus diandrus*, which was present in the resident seed bank. The other seeded non-native annual grasses (Table 1), which readily establish in many similar areas of California, did not establish in these plots presumably due to competition with *L. multiflorum* and *B. diandrus*.

Invasion of Early-Season Communities

Centaurea solstitialis established but was not dominant (16% cover) in AG + CS plots in summer 2003, the first

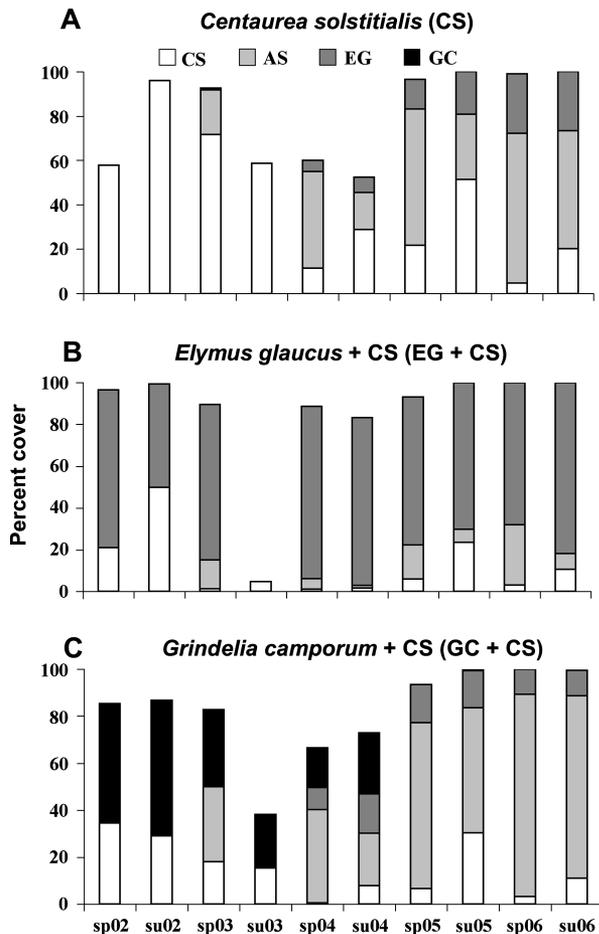


Figure 2. Percent cover from spring 2002 (sp02) through summer 2006 (su06) in a monocultures of (A) *Centaurea solstitialis* (CS), (B) *Elymus glaucus* with CS (EG + CS), and (C) *Grindelia camporum* with CS (GC + CS) showing *G. camporum* (GC), *E. glaucus* (EG), annual species (AS), and *C. solstitialis* (CS). Summer 2003 cover values only include *C. solstitialis* and *G. camporum*.

season after seeding (Fig. 1A). This level of infestation was less than CS in monoculture in its first year of establishment (Fig. 2A) and statistically less than CS alone during the same summer 2003 time period (Table 2). By the second spring and summer (2004) after seeding, *C. solstitialis* was the most dominant species present in the AG + CS plots and even the AG plots that were not seeded with *C. solstitialis* (Fig. 1B). By 2004, the level of *C. solstitialis* infestation in the AG plots was not significantly different than the AG + CS plots (Table 3). Because there was no residual *C. solstitialis* seed bank present prior to the establishment of the study, the unseeded plots presumably were infested with *C. solstitialis* from adjacent seeded communities. In both the AG and the AG + CS plots, *C. solstitialis* cover peaked at greater than 80 by summer 2005.

Annual forb communities (Fig. 1C–D) were also rapidly invaded by *C. solstitialis*. In overseeded plots (AF + CS), *C. solstitialis* cover peaked at 65% the second year following seeding (summer 2003; Fig. 1C), whereas in unseeded plots (AF), *C. solstitialis* did not become dominant until 2004 and peaked at 84% cover in summer 2005 (Fig. 1D). *Centaurea solstitialis* cover was greater in seeded plots through summer 2003 but was significantly greater in unseeded plots in 2004 and 2005 (Table 3). After reaching peak cover, *C. solstitialis* declined in both AF + CS and AF plots. In summer 2003 and 2004, *C. solstitialis* cover was not significantly different in AF + CS plots versus CS monocultures (Table 2). In CS monoculture plots (Fig. 2A), *C. solstitialis* cover peaked at 96% the year after seeding (2002), declined to 29% by summer 2004, peaked again at 50% in summer 2005, and declined the following year to less than 20%. *Centaurea solstitialis* populations commonly fluctuate with peak infestation years followed by reduced cover in subsequent years (Kyser & DiTomaso, personal observation).

Interestingly, in years where *C. solstitialis* cover was significantly different between CS and AG + CS plots after the first year of establishment (2003), *C. solstitialis* cover was always higher in the AG + CS plots (Table 2). The opposite was true for CS versus AF + CS plots.

Invasion of Late-Season Communities

Unlike the annual plant communities, *C. solstitialis* was unable to dominate in either the seeded or unseeded native perennial communities (Fig. 1E–H). *Centaurea solstitialis* cover in plots with native perennials was always lower than in CS-only plots and was significantly different in most years (Table 2). By comparison, *C. solstitialis* cover was rarely different between seeded and unseeded NP or FP plots (Table 3).

In plant communities with perennial grasses, *E. glaucus* was the dominant species (Fig. 1E–H). However, *E. glaucus* establishment was delayed by annual species in the mixed FP communities, as compared to NP communities. *Elymus glaucus* cover was greater when planted alone or seeded with *C. solstitialis* (EG + CS) from 2002 to 2004 compared

Table 2. Linear contrasts of *Centaurea solstitialis* cover between CS monocultures and mixed plant communities (AG = annual grasses; AF = annual forbs; NP = native perennials; FP = annual forbs and perennials; EG = *Elymus glaucus*; GC = *Grindelia camporum*; CS = *C. solstitialis*).

Treatment Contrast	2002		2003		2004		2005		2006	
	Spring (<i>p</i> < 0.0001, <i>n</i> = 40)	Summer (<i>p</i> < 0.0001, <i>n</i> = 50)	Spring (<i>p</i> < 0.0001, <i>n</i> = 50)	Summer (<i>p</i> < 0.0001, <i>n</i> = 60)	Spring (<i>p</i> < 0.0001, <i>n</i> = 60)	Summer (<i>p</i> < 0.0001, <i>n</i> = 60)	Spring (<i>p</i> < 0.0001, <i>n</i> = 60)	Summer (<i>p</i> < 0.0001, <i>n</i> = 60)	Spring (<i>p</i> 0.119, <i>n</i> = 32)	Summer (<i>p</i> 0.007, <i>n</i> = 32)
CS vs. AG + CS	N/A	N/A	N/A	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> 0.923	<i>p</i> < 0.0001	<i>p</i> 0.0001	N/A	N/A
CS vs. AF + CS	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> 0.205	<i>p</i> 0.308	<i>p</i> 0.233	<i>p</i> 0.010	<i>p</i> 0.001	N/A	N/A
CS vs. NP + CS	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> 0.077	<i>p</i> 0.025	<i>p</i> 0.582	<i>p</i> 0.379	<i>p</i> 0.651	<i>p</i> 0.149
CS vs. FP + CS	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> 0.045	<i>p</i> 0.020	<i>p</i> 0.006	<i>p</i> 0.0004	<i>p</i> 0.344	<i>p</i> 0.042
CS vs. EG + CS	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> 0.071	<i>p</i> 0.010	<i>p</i> 0.040	<i>p</i> 0.017	N/A	N/A
CS vs. GC + CS	<i>p</i> 0.004	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> 0.057	<i>p</i> 0.045	<i>p</i> 0.048	<i>p</i> 0.064	<i>p</i> 0.880	<i>p</i> 0.431

N/A = data not available. In each row, italicized *p* values indicate higher *C. solstitialis* cover in CS monocultures, and bolded values are significant at *p* < 0.05.

Table 3. Linear contrasts of *Centaurea solstitialis* cover between mixed plant communities (AG = annual grasses; AF = annual forbs; NP = native perennials; FP = annual forbs and perennials; EG = *Elymus glaucus*; GC = *Grindelia camporum*; CS = *C. solstitialis*) with and without CS.

Treatment Contrast	2002		2003		2004		2005		2006	
	Spring (<i>p</i> 0.072, <i>n</i> = 24)	Summer (<i>p</i> < 0.0001, <i>n</i> = 30)	Spring (<i>p</i> < 0.0001, <i>n</i> = 30)	Summer (<i>p</i> < 0.0001, <i>n</i> = 40)	Spring (<i>p</i> < 0.0001, <i>n</i> = 40)	Summer (<i>p</i> 0.0002, <i>n</i> = 40)	Spring (<i>p</i> < 0.0001, <i>n</i> = 40)	Summer (<i>p</i> < 0.0001, <i>n</i> = 40)	Spring (<i>p</i> 0.536, <i>n</i> = 20)	Summer (<i>p</i> 0.441, <i>n</i> = 20)
AG vs. AG + CS	N/A	N/A	N/A	<i>p</i> 0.033	<i>p</i> 0.741	<i>p</i> 0.641	<i>p</i> 0.0003	<i>p</i> 0.082	N/A	N/A
AF vs. AF + CS	<i>p</i> 0.007	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> 0.0002	<i>p</i> < 0.0001	<i>p</i> < 0.0001	N/A	N/A
NP vs. NP + CS	<i>p</i> 0.085	<i>p</i> 0.407	<i>p</i> 1.000	<i>p</i> 0.968	<i>p</i> 0.833	<i>p</i> 0.714	<i>p</i> 0.022	<i>p</i> 0.0001	<i>p</i> 0.753	<i>p</i> 0.658
FP vs. FP + CS	<i>p</i> 0.085	<i>p</i> 0.015	<i>p</i> 1.000	<i>p</i> 0.747	<i>p</i> 1.000	<i>p</i> 0.714	<i>p</i> 0.870	<i>p</i> 0.115	<i>p</i> 0.189	<i>p</i> 0.122

In each row, italicized *p* values indicate higher *C. solstitialis* cover in mixed plant communities without CS, and bolded values are significant at *p* < 0.05.

to the mixed communities with native perennials (Table 4). *Centaurea solstitialis* was competitive with *E. glaucus* in monoculture in the first summer after seeding and then declined in subsequent years (Fig. 2B). Overall, *E. glaucus* became the dominant species in all treatments where it was in the seeding mix.

Once established in the seeded plots, *E. glaucus* spread to most other communities (Figs. 1C–D & 2A, C). Individual *E. glaucus* plants were first identified (1% cover) in spring 2003 in the CS-only plots (data not shown). By

2006, *E. glaucus* cover reached 27% in CS plots. Satellite *E. glaucus* plants appeared in all other plots by summer 2005 (Figs. 1 & 2).

By summer 2002, *G. camporum* cover ranged from 40 to 60% in mixed native perennial communities and GC + CS (Figs. 1E–H & 2C) and was not significantly different in communities with and without CS (Table 5). In subsequent years, however, *G. camporum* cover declined, and by 2005, it was no longer present in any of the plots where it had previously established, including GC + CS (Fig. 2).

Table 4. Linear contrasts of *Elymus glaucus* cover between mixed plant communities (AG = annual grasses; AF = annual forbs; NP = native perennials; FP = annual forbs and perennials; EG = *E. glaucus*; GC = *Grindelia camporum*; CS = *Centaurea solstitialis*) with and without *C. solstitialis*, and between *E. glaucus* monocultures (EG + CS) and mixed communities with *C. solstitialis* (NP + CS and FP + CS).

Treatment Contrast	2002		2003		2004		2005		2006	
	Spring (<i>p</i> < 0.0001, <i>n</i> = 40)	Summer (<i>p</i> < 0.0001, <i>n</i> = 50)	Spring (<i>p</i> < 0.0001, <i>n</i> = 50)	Summer	Spring (<i>p</i> < 0.0001, <i>n</i> = 60)	Summer (<i>p</i> < 0.0001, <i>n</i> = 60)	Spring (<i>p</i> < 0.0001, <i>n</i> = 60)	Summer (<i>p</i> < 0.0001, <i>n</i> = 60)	Spring (<i>p</i> < 0.0001, <i>n</i> = 32)	Summer (<i>p</i> < 0.0001, <i>n</i> = 32)
NP vs. NP + CS	<i>p</i> 0.017	<i>p</i> 0.149	<i>p</i> 0.006	N/A	<i>p</i> 0.031	<i>p</i> 0.033	<i>p</i> < 0.0001	<i>p</i> 0.0002	<i>p</i> 0.072	<i>p</i> 0.113
FP vs. FP + CS	<i>p</i> 1.000	<i>p</i> 0.762	<i>p</i> 0.942	N/A	<i>p</i> 0.189	<i>p</i> 0.052	<i>p</i> 0.038	<i>p</i> 0.532	<i>p</i> 0.295	<i>p</i> < 0.0001
EG + CS vs. NP + CS	<i>p</i> 0.387	<i>p</i> 0.860	<i>p</i> < 0.0001	N/A	<i>p</i> 0.0004	<i>p</i> 0.0002	<i>p</i> 0.010	<i>p</i> 0.025	N/A	N/A
EG + CS vs. FP + CS	<i>p</i> < 0.0001	<i>p</i> < 0.0001	<i>p</i> < 0.0001	N/A	<i>p</i> 0.001	<i>p</i> 0.007	<i>p</i> 0.634	<i>p</i> 0.362	N/A	N/A

In each row, italicized *p* values indicate higher *E. glaucus* cover in communities without *C. solstitialis* or in *E. glaucus* monocultures, and bolded values are significant at *p* < 0.05.

Table 5. Linear contrasts of *Grindelia camporum* cover between mixed plant communities (AG = annual grasses; AF = annual forbs; NP = native perennials; FP = annual forbs and perennials; EG = *Elymus glaucus*; GC = *G. camporum*; CS = *Centaurea solstitialis*) with and without *C. solstitialis*, and between *G. camporum* monocultures (GC + CS) and mixed communities with *C. solstitialis* (NP + CS and FP + CS).

Treatment Contrast	2002		2003		2004		2005
	Spring (<i>p</i> < 0.0001, <i>n</i> = 40)	Summer (<i>p</i> < 0.0001, <i>n</i> = 40)	Spring (<i>p</i> < 0.0001, <i>n</i> = 50)	Summer (<i>p</i> < 0.0001, <i>n</i> = 60)	Spring (<i>p</i> 0.016, <i>n</i> = 60)	Summer (<i>p</i> 0.003, <i>n</i> = 60)	Summer (<i>p</i> 0.041, <i>n</i> = 60)
NP vs. NP + CS	<i>p</i> 0.072	<i>p</i> 0.881	<i>p</i> 0.944	<i>p</i> 0.005	<i>p</i> 0.670	<i>p</i> 0.374	<i>p</i> 0.895
FP vs. FP + CS	<i>p</i> 0.973	<i>p</i> 0.215	<i>p</i> 0.033	<i>p</i> < 0.0001	<i>p</i> 0.189	<i>p</i> 0.176	<i>p</i> 0.895
GC + CS vs. NP + CS	<i>p</i> 0.0007	<i>p</i> < 0.0001	<i>p</i> 0.0003	<i>p</i> < 0.0001	<i>p</i> 0.132	<i>p</i> 0.028	<i>p</i> 0.895
GC + CS vs. FP + CS	<i>p</i> 0.006	<i>p</i> < 0.0001	<i>p</i> 0.001	<i>p</i> < 0.0001	<i>p</i> 0.218	<i>p</i> 0.139	<i>p</i> 1.000

In each row, italicized *p* values indicate higher *G. camporum* cover in communities without *C. solstitialis* or in *G. camporum* monocultures, and bolded values are significant at *p* < 0.05.

Discussion

Early-Season Communities

In this study, *Centaurea solstitialis* readily invaded non-native annual grass and native annual forb communities. *Centaurea solstitialis* became dominant in AG and AG + CS plots within 1 year after introduction. Likewise, *C. solstitialis* rapidly invades California rangelands dominated by non-native annual grasses (Roché & Roché 1991; Roché et al. 1994; DiTomaso 2000). The invasion trajectory of *C. solstitialis* in annual grasslands is heavily influenced by the amount of spring precipitation (Enloe et al. 2004; Young 2007). In this study, spring (March to May) precipitation during 2004 was 16% of the long-term average, whereas spring 2005 was 100% of the long-term average. As a result, *C. solstitialis* cover in AG and AG + CS plots was higher in spring (57–61%) than summer (25–29%) 2004, likely a result of self-thinning following the dry spring. However, following a normal spring precipitation (2005), *C. solstitialis* cover increased from spring to summer. By contrast, in the CS monoculture, *C. solstitialis* cover was apparently too low (~11%) to experience self-thinning in 2004 (Kyser & DiTomaso, personal observation) and actually increased in summer despite the low spring rainfall.

Native annual forbs dominated all early-season AF and the early/late-season FP plots in spring 2002 (50–95%) but then declined in subsequent years and did not establish outside their plots. Although somewhat better competitors with *C. solstitialis* than the non-native annual grasses, the native annual forbs were unable to prevent invasion of *C. solstitialis* or the establishment of *E. glaucus*. We observed seed production in all early-season species and therefore do not attribute their decline to seed limitation. Both non-native annual grasses and native annual forbs are functionally dissimilar to *C. solstitialis* in timing of resource acquisition and were not expected to resist invasion.

Cover of *C. solstitialis* in CS plots reached a peak in the season following seeding (summer 2002) and declined in all subsequent years. This may have been partly due to intense intraspecific competition (Roché et al. 1997). Furthermore, the accumulation of *C. solstitialis* standing and

ground litter after 2002 reduced light penetration through the canopy, potentially suppressing *C. solstitialis* growth in the following years. Light at the soil surface in May and July 2002 (the first year of establishment, with high *C. solstitialis* cover and no thatch) was 13 and 26% of full sunlight, respectively (Young 2007). From 2003 to 2005, however, light at the soil surface in CS plots ranged between 3 and 6% during May and July. During these years, *C. solstitialis* cover decreased to between 21 and 44%. *Centaurea solstitialis* has been shown to require high light levels (>20% of full sun) to survive (Roché et al. 1994; DiTomaso et al. 2003).

Late-Season Communities

Plant species that are functionally similar to *C. solstitialis* are expected to provide the highest level of competitive resistance to invasion (Zavaleta & Hulvey 2007). However, *G. camporum*, selected for this study due to its functional similarities to *C. solstitialis*, proved to be a poor competitor over time not only with *C. solstitialis* but also with other annual and perennial species. Thus, *G. camporum* appears to be an early-succession species and a good colonizer in newly restored or disturbed plant communities but is not tolerant to mowing or heavy grazing. *Grindelia camporum* is not sustainable in these systems and is not likely to provide long-term suppression of *C. solstitialis*.

Establishment and subsequent dominance of *E. glaucus* in native plant communities suppressed invasion by *C. solstitialis*. Although different from *C. solstitialis* in its morphology, taxonomic classification, life cycle, root architecture, and phenology, *E. glaucus* is functionally similar to *C. solstitialis* in its timing of resource acquisition. Persistence of *E. glaucus* in the Central Valley is due to its extensive root system capable of accessing deep soil moisture and, thus, avoiding competition with shallow-rooted annual species (Dyer & Rice 1997; Clary et al. 2004). However, establishment of perennial grasses is suppressed by competition from non-native annual species during the critical period of seedling development (Enloe et al. 2005). Not surprisingly, rangelands throughout much of California are

dominated by non-native annual grass species, which generally resist reestablishment of native perennial grasses, including *E. glaucus*.

Colonization by *E. glaucus*, where it was not intentionally seeded, appears to depend on the functional group composition of the invaded plant community. The eventual dominance of *E. glaucus* in FP and NP plant communities, with and without *C. solstitialis*, demonstrates its competitive potential. Timing of resource utilization has a greater impact on competitive interaction than do morphological or phenological similarities (Jackson & Roy 1986; Rice 1989; Holmes & Rice 1996).

Conclusions

Under our site conditions, seeded communities containing *Elymus glaucus* resisted invasion of *Centaurea solstitialis* for at least 5 years after establishment. Within 3 years of seeding, *E. glaucus* became dominant in all communities where it was planted. Moreover, it spread from seeded sites to establish in other plots, including those planted only to *C. solstitialis*. *Grindelia camporum*, a late-season native perennial forb with a similar growth habit to *C. solstitialis*, established rapidly but was replaced by other species within 3 years.

Functional differences among plant species can influence their interaction and may affect their ability to resist non-native plant invasion. Species from a common functional group may differ in their ability to compete within a community because of other environmental constraints (Zavaleta & Hulvey 2007). Under the conditions present in this study, *E. glaucus*, which is functionally similar in resource utilization to *C. solstitialis*, was able to not only resist invasion but also proliferate.

With *C. solstitialis* replacing populations of non-native annual grasses throughout much of California's grasslands, the management and ecological benefits of native perennial grasses, especially *E. glaucus*, will be of increasing importance (Rossiter et al. 2003; De Luis et al. 2004; Jankauskas et al. 2004). In addition to erosion control and reduced wildfire hazard, establishment of native perennial grass communities has the potential benefit of resisting invasion by non-native species.

Implications for Practice

- Communities with high species diversity are not necessarily the most resistant to invasion.
- High species diversity in seed mixes will not always result in a stable high-diversity community.
- Grassland restoration programs should consider using species that are not only capable of establishing and proliferating but also overlap in their timing of resource acquisition with potential high-risk invaders.

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