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Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub

Robert D. Cox† and Edith B. Allen*

Department of Botany and Plant Sciences and Center for Conservation Biology, University of California, Riverside, CA 92521, USA

Summary

1. Restoration of semi-arid shrub ecosystems often requires control of invasive grasses but the effects of these grass-control treatments on native and exotic forbs have not been investigated adequately to assess long-term stability. In southern California, coastal sage scrub (CSS) vegetation is one semi-arid shrub community that has been invaded extensively by both exotic grasses and exotic forbs and is a target for restoration.

2. We studied the effects of grass-specific herbicide, thatch removal plus herbicide and mowing on native and exotic species in a heavily invaded CSS community. We followed this grass-control experiment for 6 years to assess the stability of such treatments. We also added a soil disturbance experiment to investigate the potential influence of thatch removal and soil disturbance on exotic and native grasses and forbs.

3. In the grass-control experiment, treatments reduced exotic grass cover to differing degrees. Three years of mowing resulted in lower exotic grass cover, but only for 2 years. Both herbicide and herbicide plus thatch removal reduced exotic grasses more than mowing, and effects persisted for longer. However, reducing exotic grass cover increased seeded species only during the year of seeding. In addition, plots where exotic grasses were controlled by herbicides also experienced increases in exotic forb cover.

4. In the soil-disturbance experiment, treatments did not increase cover of native species, although plots in which soil was disturbed did have less exotic grass cover. In both experiments, plots observed in years with different rainfall experienced widely varied plant cover, emphasizing the influence that precipitation exerts in these systems.

5. *Synthesis and applications*. In restoration of semi-arid shrub ecosystems, grass control can reduce exotic grasses over the short-term. However, recovery of grasses in the longer term indicates that restoration does not form a new stable state. Restoration and management of semi-arid shrublands may therefore require continual grass control. Exotic forbs should also be considered for control, as they may increase when exotic grasses are removed. Yearly variations in precipitation confound determination of successful restoration efforts, and require long-term observations to detect the response of native species to treatments.

Key-words: *Artemisia californica*, *Bromus* spp., exotic forbs, grass control, herbicide application, invasive species, soil disturbance

Introduction

Ecological succession has been considered a suitable model for understanding the restoration of disturbed plant communities (Luken 1990; Young, Petersen & Clary 2005). However, in areas that are heavily invaded by non-native species, natural successional processes may not be adequate for full restoration (Suding, Gross & Houseman 2004). In such cases, restoration scientists and practitioners have looked to other theories of plant community development, such as state and transition models, competitive hierarchies and community assembly theory, to guide restoration efforts. Such models take into account the disproportionate influence that invasive species

*Correspondence author. E-mail: edith.allen@ucr.edu
†Present address: USDA Forest Service, Rocky Mountain Research Station, 322 E. Front Street, Suite 401, Boise, ID 83702, USA.

appear to have on some community types (Choi 2004; Suding, Gross & Houseman 2004; Keddy 2005; Young, Petersen & Clary 2005).

Understanding this influence is important because, since European contact, exotic annual plants have invaded many Mediterranean-type ecosystems (Fox 1990; D'Antonio & Vitousek 1992; Pimentel, Zuniga & Morrison 2005). In the USA, these invasions have resulted in the conversion of large areas from semi-arid shrub communities into stable communities dominated by annual grasses of Mediterranean origin (Mack 1981; Laycock 1991; Allen *et al.* 1998; Minnich & Dezzani 1998). Because many invaded plant communities also experience altered fire regimes and loss of biodiversity (D'Antonio & Vitousek 1992; Mack & D'Antonio 1998), they are often targets for restoration and conservation (Bowler 1990; Pellant, Abby & Karl 2004). However, the invasive species generally persist (Stylinski & Allen 1999; Spooner, Lunt & Robinson 2002) and few long-term studies have been conducted to determine whether restoration treatments will create a new stable state or whether control of exotic species must become part of the continuous management plan for conservation reserves.

Southern California coastal sage scrub (CSS) is one semi-arid shrub community that has been invaded extensively by exotic grasses. CSS vegetation consists of drought-deciduous, seasonally dimorphic shrubs and subshrubs, with a diverse understorey of herbaceous annuals (Westman 1981; O'Leary, Murphy & Brussard 1992; DeSimone 1995), and occurs on lower altitude sites in southern California (Westman 1981; O'Leary, Murphy & Brussard 1992; Rubinoff 2001). In addition, CSS is habitat for more than 200 plant and animal species that are currently endangered, threatened or of 'special concern' (O'Leary, Murphy & Brussard 1992; Bowler 2000; Tibor 2001).

As is common in many plant communities that harbour high levels of diversity and rare species, human activities have greatly reduced the extent of CSS. Estimates of CSS loss range from 36% to 85% (Klopatek *et al.* 1979; Westman 1981; O'Leary 1995) and qualify it as one of the most endangered vegetation types in the USA (Klopatek *et al.* 1979; Noss, Laroei & Scott 1995; Rubinoff 2001). Such losses are compounded by many threats, such as development of private property (O'Leary 1995), airborne pollution (including nitrogen deposition) (Westman 1985; Cione, Padgett & Allen 2002), fragmentation (O'Leary 1995; Zink *et al.* 1995) and reduced fire return intervals (Keeley 1986; Minnich & Dezzani 1998).

Although there are many factors implicated in the decline of CSS and other semi-arid shrublands, it is clear that Mediterranean annual grasses play a significant role. They are efficient competitors against native forbs and shrubs in many areas, including the USA (Schultz, Launchbaugh & Biswell 1955; Bush & Van Auken 1989), South Africa (Midoko-Iponga, Krug & Milton 2005), Spain (Clary *et al.* 2004) and Israel (Litav, Kupernik & Orshan 1963). Competition from exotic annual grasses may be particularly important in plant communities such as CSS, where native annual forbs are a significant component. In addition, native plant communities invaded by these grasses experience changes in resource availability, nutrient cycling, species composition and even disturbance regimes (D'Antonio & Vitousek 1992; Mack & D'Antonio 1998). In many semi-arid areas of southern California, invasion of exotic annual grasses appears to contribute to degradation and loss of native communities by reducing light at the soil surface (Eliason & Allen 1997), reducing soil moisture (Davis & Mooney 1985; Eliason & Allen 1997) and increasing the frequency of fire (Keeley 1986; Minnich & Dezzani 1998).

For these reasons, grass-control treatments such as mowing, herbicide application and soil disturbance are often necessary when restoration of CSS is attempted (Eliason & Allen 1997; Allen *et al.* 2000; Cione, Padgett & Allen 2002; Gillespie & Allen 2004). Mowing has been used in many plant communities to control exotic grasses and allow establishment of native species. The effects of mowing are variable and can increase (Maron & Jefferies 2001) or decrease (Kimball & Schiffman 2003) plant diversity, with the outcome presumably influenced by the identity of the targeted species, the timing and intensity of the mowing treatment and also by various abiotic factors (Proulx & Mazumder 1998; Stohlgren, Schell & Heuvel 1999). Herbicides have been used to control exotic grass species in semi-arid shrublands, including sagebrush–grass steppe in the Great Basin (Cox & Anderson 2004) and CSS in southern California (Cione, Padgett & Allen 2002; Allen *et al.* 2005). Soil disturbances and litter levels may have an important influence on diversity in annual grasslands (Hobbs & Hobbs 1987; Peart 1989; Carson & Peterson 1990; Gillespie & Allen 2004) and in CSS (DeSimone & Zedler 1999). These factors have the potential to impact seed-bed characteristics that are important to germinating and establishing species, including light, temperature and soil moisture, and thus influencing the availability of 'safe sites' for species recruitment (Harper *et al.* 1961; Grubb 1977; Fowler 1988). For example, soil scalping and disturbance facilitated establishment of a native grass species in *Eucalyptus* woodlands that had been degraded through invasion of exotic annual grasses and forbs (Cole, Lunt & Koen 2004).

Although exotic grasses are often the focus of restoration weed control efforts, little is known about how these treatments influence exotic forbs that may be present at a site. Like exotic grasses, exotic forbs have been very successful invaders (Minnich & Dezzani 1998; DiTomaso 2000) but their effects on CSS and similar shrub communities are not well understood. Species of *Erodium* may have been among the first exotic plants to become naturalized in California (Mensing & Byrne 1998) and are now nearly ubiquitous across wide areas of the western USA. Although some native species may be less affected by competition with exotic species of *Erodium* than with species of exotic grasses (Gillespie & Allen 2004), *Erodium* may reduce or slow emergence of other native perennial species (Gordon *et al.* 1989; Gordon & Rice 1993).

It is not well understood how removal of exotic grasses may affect the exotic forb species that have also been proven successful at invading these habitats. For example, *Erodium* *cicutarium* (L.) Aiton increased under grass clipping in some studies (Kimball & Schiffman 2003; Allen *et al*. 2005). Species of *Erodium* may also utilize soil disturbance patches during invasion and recruitment (Young *et al*. 1981; Rice 1985) and *Erodium* colonization is enhanced by litter removal (Rice 1987). From a management standpoint, it is important to understand whether exotic forbs increase under grass control regimes and how such increases might influence native species.

Finally, many published restoration studies report results after only 2 or 3 years, but effects of many restoration treatments may take longer. In particular, responses in unpredictable environments, such as under high variability in precipitation, are more likely to be observed and correctly interpreted when field observations are done for longer periods. Such longer term monitoring of restoration sites allows researchers and managers to determine whether restoration efforts have successfully created new vegetation states that are stable enough to resist subsequent re-invasion of non-native species. We investigated the effects of three grass-control methods (herbicide, thatch removal plus herbicide and mowing) on the exotic grasses, exotic forbs and native species in a heavily invaded CSS patch and observed the site for 6 years. Because preliminary results indicated that soil disturbance and thatch removal could be important for improving recruitment of native species in CSS areas invaded by exotic grasses, we also investigated the effects of soil disturbance and thatch removal on adjacent annual grassland.

Materials and methods

STUDY SITE

The Shipley Reserve was established within the Western Riverside County Multi-species Habitat Reserve, California, USA, in 1992 to provide habitat connectivity between two reservoirs. The reserve includes several vegetation types, including oak woodland, chaparral, CSS and annual grassland. CSS portions of the reserve are heavily invaded by annual grasses and forbs, including *Avena fatua*, *Bromus diandrus*, *Bromus hordeaceus*, *Bromus madritensis* ssp. *rubens*, *Erodium brachycarpum*, *Erodium cicutarium* and *Hirschfeldia incana* (nomenclature follows Hickman 1993). This study, consisting of two experiments, was established on approximately 2 ha of a south-facing (5–10%) slope at 33°39′28″N and 116°59′42″W and approximately 677 m altitude on the Shipley Reserve. Vegetation at this portion of the reserve consists of sparse CSS [less than 30% average cover of *Artemisia californica* Less., *Eriogonum fasciculatum* (Benth) Torr. & A. Gray and *Salvia apiana* Jeps.], with an understorey of exotic annuals and native forbs. Cover of mature shrubs at the site did not change during the study. The history of early European settlement of the area is not well documented but at this location included extensive grazing of cattle and sheep coupled with clearing of native vegetation in the valley bottoms (Allen *et al*. 2005).

The average precipitation (over 19 years) of the area has been 247 mm, occurring during the winter growing season. Summers are hot and dry, as is characteristic of Mediterranean-type ecosystems. Five of the 6 years of this study received lower than average July–June precipitation (Fig. 1). During the 2002 growing season, precipitation was less than 35% of the average.

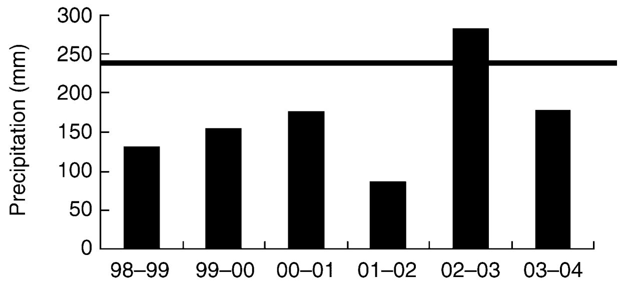

Fig. 1. 1 July–June 30 precipitation at the University of California Riverside CIMIS (California Irrigation Management Information System) weather station, Riverside, County, California, USA, from 1999 to 2004 (www.cimis.water.ca.gov, accessed May 2006). Dark line represents 19-year average precipitation (= 247 mm).

EXPERIMENTAL DESIGN

Grass-control experiment

The responses of various species groups (exotic grasses, exotic forbs, native forbs) to common weed control methods were tested in a randomized block design: four 10 × 10-m plots, each assigned to one method of grass control, were replicated in five blocks across about 1·5 ha on a south-facing slope. Three treatments (plus a control of no treatment) were tested: herbicide application, thatch removal plus herbicide application and mowing (with a hand-held weed trimmer).

For the first, treatment, herbicide application, Fusilade II™ (fluazifop-P-Butyl), a post-emergence, grass-specific herbicide with little soil residual activity (Tu, Hurd & Randall 2001), was applied with a hand-sprayer at the manufacturer's lowest recommended rate. Herbicide was applied in two consecutive years (March 1999 and April 2000).

In the second treatment, thatch removal was carried out to increase the contact of the herbicide with actively translocating grasses. Cured grass stalks (i.e. standing culms from the same year's growing season) were mown with a hand-held weed trimmer and then removed by raking, along with the previous years' build-up of thatch. Thatch consists of the lodged and flattened culms and debris from previous years' growth and is composed almost entirely of exotic grass stalks and leaves, as the remains of herbaceous forbs (both native and exotic) disintegrate quickly and rarely persist from year to year. Raking was done so as to not disturb the soil surface. Thatch removal occurred in October 1999 and herbicide application (as above) occurred in March 1999 and April 2000.

For the third treatment, mowing was accomplished with a hand-held weed trimmer in early spring before seed set, to reduce the next generation of exotic grasses. Three applications were used: May 1999, April 2000 and March 2001. Because the May 1999 application occurred after data collection in that year (April 1999), mowing data were not analysed until the second year (2000).

In the third year of the study, one half of each plot was randomly selected and seeded at a high rate with a mix of species (shrubs and forbs) native to the area (Table 1). Seeds were donated by S. & S. Seed Co. (Carpinteria, CA) and were collected locally. Each plot to be seeded was lightly raked to scarify the soil and seed was broadcast by hand after rain on 9 January 2001.

Soil disturbance experiment

To test the effects of thatch removal and soil disturbance on emergence of native species, a split-plot experiment was established in a

Table 1. Grass-control experiment: species and seeding rates for species seeded on 9 January 2001 at the Shipley Reserve, Riverside Co., California, USA. Seeding rates are given in numbers of pure live seed (PLS) sown per m^2. Nomenclature follows Hickman (1993)

Species	Life span	Growth form	Seeding rate (PLS m^{-2})
Artemisia californica	Perennial	Shrub	121·9
Castilleja exserta	Annual	Forb	203·5
Dichelostemma capitatum	Perennial	Forb	3·2
Eriogonum fasciculatum var. *foliolosum*	Perennial	Shrub	94·8
Gutierrezia californica	Perennial	Shrub	15·0
Lasthenia californica	Annual	Forb	167·4
Lupinus bicolor	Annual	Forb	6·9
Lupinus sparsiflorus	Annual	Forb	13·5

grass-dominated area adjacent to the grass-control experiment. Occupying about 0·2 ha, this area is thought to have once supported CSS shrubs but is now dominated by exotic grasses and forbs and produces a thick thatch of exotic grass litter, allowing reliable contrasts between treatment effects. The experiment was begun in 2003 and repeated in 2004. Plots, measuring 2 × 2 m, were established in 10 blocks, with three treatment plots per block. Treatments were soil disturbance (with thatch removal), thatch removal (but no soil disturbance) and control (no soil disturbance or thatch removal). In soil-disturbance plots, thatch was removed and the soil was disturbed by heavily raking with a hand-rake. In thatch-removal plots, thatch was removed with a rake, taking care not to disturb the soil surface. Control plots were left undisturbed. After treatment, half of each plot was selected randomly and seeded with a seed mix equivalent to the previous experiment (Table 1). After treatments had been applied, solar radiation at ground level in each plot was measured in February 2003 and January 2004 with a 1-m line quantum sensor (Li 191; LI-COR Biosciences, Lincoln, NB) to evaluate differences in solar radiation at the soil surface.

DATA ANALYSIS

In both experiments, cover data (estimated to the nearest 1%) were collected for all species of exotic grass, exotic forbs, native forbs, native shrubs and seeded species, as well as for litter. For the grass-control experiment, data were collected in five permanent 0·5 × 1·0-m quadrats within each main plot in late spring from 1999 to 2004. After seeding in 2001, four additional quadrats were sampled each year. In the soil disturbance experiment, data were collected in four 0·5 × 1·0-m subplots in each main plot in late spring from 2003 to 2004. Species were placed into functional groups of exotic grass, exotic forbs, native forbs and native shrubs. Such an approach is useful in studies of biodiversity (Suding *et al.* 2005) and has been used for comparison of native vs. exotic vegetation responses in studies of annual grassland and CSS (Gillespie & Allen 2004; Allen *et al.* 2005). Species richness (i.e. the number of species) was also calculated for each sample. Cover data were arcsine transformed. Data for the grass-control experiment were analysed separately for each year because treatments were repeated in different years. Solar radiation data for the soil disturbance experiment were also analysed separately for each year. Analysis of variance was performed in JMP (SAS Institute 2006) and significant differences were accepted at $P = 0·05$. Block effects and interactions were occasionally significant but no consistent pattern was evident, i.e. different blocks had higher or lower cover of grasses or forbs in different years, reflecting the impacts of variable precipitation on annual plants but not indicative of treatment.

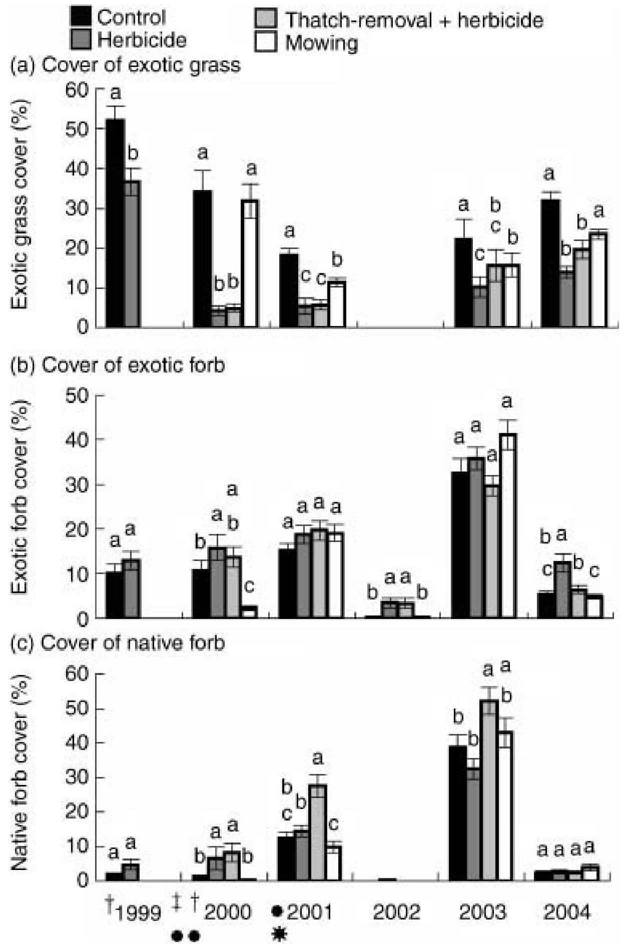

Fig. 2. Grass-control experiment: (a) percentage cover of exotic grass, (b) percentage cover of exotic forb and (c) percentage cover of native forb in treatment plots in Riverside County, California, USA, from 1999 to 2004. Lowercase letters indicate within-year significant differences ($P = 0·05$). Bars indicate standard error. Typographic symbols indicate timing of treatments: †, herbicide treatments; ‡, thatch removal; circles, mowing; stars, seeding. In 1999, herbicide was the only treatment tested. All treatments were tested in subsequent years.

Results

GRASS-CONTROL EXPERIMENT

Precipitation levels influenced cover of both grasses and forbs during the period of the study. Grass cover declined each year from 1998 to 2002, when precipitation was less than 100 mm (Figs 1 and 2a). The 2003 growing season, however, received average or slightly above-average precipitation, and cover of exotic grasses, exotic forbs and native forbs began to recover (Fig. 2a–c). The final year of the study, 2004, once again had below average precipitation, and once again the forbs, both exotic and native, displayed very low cover.

All grass-control treatments reduced cover of exotic grass for at least 1 or 2 years (Fig. 2a). Mowing was not effective the first year after treatment (2000), as grasses recovered to control levels by the time data were collected in April. Mown plots had 11·4% cover of exotic grass in 2001 (after 3 years of treatment) and 15·7% in 2003 (2 unmown years following 3 years of treatment), compared with 18·1% and 22·1% cover during those years in control plots. Both herbicide treatments also reduced exotic grass cover but were not different from each other. Herbicide plots had reduced grass cover in 1999, 2000, 2001, 2003 and 2004. In 2000, after 2 consecutive years of herbicide treatment, grass cover was about 4·2% in herbicide plots compared with about 34% in control plots. By 2004, 4 years after the last treatment, grass cover was still lower in herbicide plots but the difference was not as great. Thatch-removal treatments did not reduce grass cover more than herbicide alone.

Grass control also affected cover of exotic forbs, but in contrasting directions in different treatments (Fig. 2b). In 2000, after two treatments, mown plots had about 2·2% cover of exotic forbs, while control plots had 10·5% cover and herbicide plots had up to 15·7% cover of exotic forbs. This effect was only temporary; levels of exotic forb cover in mown plots became similar to control plots once treatment had ceased. Herbicide application, on the other hand, increased cover of exotic forbs in 2000, 2002 and 2004 (up to 4 years after the last herbicide treatment). Thatch removal plus herbicide application did not increase the cover of exotic forbs as much as herbicide alone; in most years, this treatment was not different from control plots.

For 3 of the 6 years of this study, native forbs had greatest cover in herbicide plots, especially in the thatch-removal treatments (Fig. 2c). In 2000, after 2 years of herbicide treatment, herbicide alone and thatch removal plus herbicide plots had up to 8·2% cover while control plots had only 1·1% cover. By 2003, 3 years after the two herbicide treatments, the thatch removal plus herbicide plots had an average of 52·3% native forb cover, compared with 38·6% in control plots. Interestingly, herbicide plots that did not receive thatch removal differed in native forb cover only in 2000; thereafter, these plots were not different from control plots. During 2003, the year of greatest native forb cover, 37 native and 14 exotic species were observed (Table 2). The cover of these individual species fluctuated greatly during the years of the study but, because most native species occurred in less than 20% of sample quadrats, statistical analysis was not performed on individual species.

Species included in the seed mix were influenced by grass-control treatments only during the first season following seeding (2001), when both mown and herbicide plots had lower cover of seeded forbs (about 3·7%) than control and thatch removal plus herbicide plots (4·8% and 6·3%, respectively). Subsequent years did not display differences. Although three species of shrubs were included in the seed mix, these shrubs failed to establish in significant numbers; only 106 shrub seedlings were observed in sample quadrats during the entire 6 years of the experiment (< 1 shrub plot^{-1}).

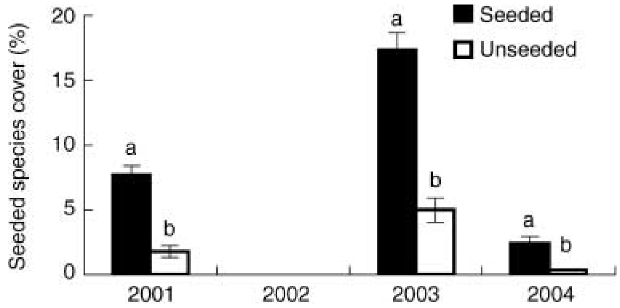

Fig. 3. Grass-control experiment: percentage cover of seeded native forbs in seeded and unseeded plots in Riverside County, California, USA, from 2001 to 2004. Seeding occurred on 9 January 2001. Lowercase letters indicate within-year significant differences ($P = 0·05$). Bars indicate standard error.

As expected, seeded species had greater cover in the seeded plots (Fig. 3) during 2001, 2003 and 2004, when seeded plots averaged 7·7%, 17·3% and 2·4% cover of native species, respectively. Native species not included in the seed mix also increased in cover in seeded plots during 2001 (data not shown), perhaps because of raking the soil surface prior to seeding. This difference was not observed in subsequent years.

Species richness was generally greatest in plots receiving herbicide (Table 3). In 2000, 2001, 2002 and 2003, plots receiving the thatch removal plus herbicide treatment displayed greater richness than control plots. Plots receiving only herbicide also displayed greater richness than control plots in 2000 and 2002.

SOIL DISTURBANCE EXPERIMENT

Solar radiation data showed that thatch removal increased the light incident at ground level (data not shown). In February 2003, solar radiation was approximately 100 µmol m^{-2} s^{-1} greater in thatch-removal plots than in control plots; solar radiation in soil-disturbance plots was not significantly different from thatch-removal or control plots. In January 2004, solar radiation was significantly different in all treatments, as control plots received only 250 µmol m^{-2} s^{-1}, thatch-removal plots received 638 µmol m^{-2} s^{-1} and soil-disturbance plots received 743 µmol m^{-2} s^{-1}.

Cover of litter had a two-way interaction between year and treatment (Fig. 4a). During both years, control plots had more than double the litter cover of thatch-removal and soil-disturbance plots. Also during both years, thatch-removal plots had up to 50% more litter than soil-disturbance plots. Litter was particularly low in treatment plots during 2004.

Over the 2 years of the experiment, cover of exotic grasses was significantly lower in soil-disturbance plots than in control and thatch-removal plots (Fig. 4b). During this time, soil-disturbance plots averaged 56% cover of exotic grass, compared with 71% in thatch-removal plots and 82% in control plots. Cover of exotic grasses was not different between the 2 years.

Cover of both exotic and native forbs was greater in 2003 than in similar plots during 2004 (data not shown). Exotic

Table 2. Grass-control experiment: species and average percentage cover observed in each treatment type during 2003, the year with the highest native forb cover, in experimental plots at the Shipley Reserve, Riverside County, California, USA. Species are alphabetized by family. *Species marked with an asterisk are perennial; others are annual with a few biennials. Species in bold were seeded in 2001. Nomenclature follows Hickman (1993)

Family	Species	Control	Herbicide	Thatch removal + herbicide	Mow
NATIVE SHRUBS					
Asteraceae	***Artemisia californica***	2·3	3·1	0·6	0·0
Polygonaceae	***Eriogonum fasciculatum***	7·4	4·0	7·8	9·6
NATIVE FORBS					
Apiaceae	*Daucus pusillus*	0·0	0·1	0·0	0·0
Asteraceae	*Filago californica*	0·2	0·2	0·8	0·5
	Hemizonia fasciculata	1·0	0·8	0·5	1·9
	Lasthenia californica	4·2	5·4	6·0	5·4
	**Lessingia filaginifolia*	0·0	0·1	0·0	0·0
	Stephanomeria exigua	0·1	0·0	0·1	0·2
	Stylocline gnaphaloides	2·2	1·7	2·0	0·8
	Uropappus lindleyi	0·4	0·0	0·8	0·6
Boraginaceae	*Amsinkia menzsiesii*	0·9	0·2	1·0	0·1
	Cryptantha intermedia	2·6	0·3	0·1	1·8
	Pectocarya linearis	1·3	0·5	1·2	0·0
	Plagiobothrys spp.	3·2	2·9	9·0	2·8
Brassicaceae	*Caulanthus heterophyllus*	0·0	0·0	0·0	0·1
	Tropidocarpum gracile	0·5	0·3	0·2	0·2
Convolvulaceae	*Calystegia macrostegia*	0·0	0·3	0·0	0·0
Crassulaceae	*Crassula connata*	1·6	2·6	2·2	1·4
Euphorbiaceae	*Eremocarpus setigerus*	0·2	0·5	0·1	0·1
Fabaceae	*Lotus hamatus*	4·1	3·8	8·9	4·4
	Lotus strigosus	5·1	4·9	8·9	12·5
	Lupinus bicolor	1·8	0·4	1·8	1·7
	Lupinus sparsiflorus	1·2	3·2	0·8	1·2
	Lupinus truncatus	1·8	0·6	0·0	1·0
Hydrophyllaceae	*Emmenanthe penduliflora*	0·4	0·0	0·1	0·3
Lamiaceae	*Salvia columbariae*	0·0	0·0	0·0	0·2
Liliaceae	***Dichelostemma capitatum***	0·2	0·7	0·7	0·5
Onagraceae	*Camissonia bistorta*	0·2	0·0	0·0	0·6
	Clarkia purpurea	0·0	0·0	0·2	0·0
Papaveraceae	*Eschscholzia californica*	1·1	0·0	0·0	0·0
Plantaginaceae	*Plantago erecta*	1·2	0·0	0·0	0·0
Polemoniaceae	*Gilia angelensis*	0·0	0·2	0·3	0·1
Portulacaceae	*Calandrinia ciliata*	1·2	1·6	4·2	2·2
	Calyptridium monandrum	0·1	0·0	1·1	2·1
Scrophulariaceae	*Antirrhinum coulterianum*	0·4	0·0	0·0	0·0
	Castilleja exserta	1·1	1·0	1·1	0·4
	Linaria canadensis	0·0	0·1	0·0	0·0
EXOTIC FORBS					
Asteraceae	*Centaurea melitensis*	0·7	0·2	0·1	0·0
	Filago gallica	1·2	0·8	1·1	0·1
	Lactuca serriola	0·2	0·0	0·0	0·0
Brassicaceae	*Hirschfeldia incana*	1·5	1·5	1·1	2·3
	Sisymbrium altissimum	5·0	2·0	3·2	5·0
Geraniaceae	*Erodium brachycarpum*	0·0	2·8	0·3	0·0
	Erodium cicutarium	23·8	25·0	22·4	33·5
	Erodium moschatum	0·0	3·5	1·4	0·3
EXOTIC GRASSES					
Poaceae	*Avena barbata*	0·1	0·2	0·3	0·1
	Bromus diandrus	2·6	0·3	0·7	0·2
	Bromus hordeaceus	0·4	0·0	0·0	0·1
	Bromus madritensis ssp. *rubens*	12·8	4·3	5·1	5·4
	Schismus barbatus	6·4	5·4	9·6	9·9
	Vulpia myuros	0·0	0·7	0·4	0·3

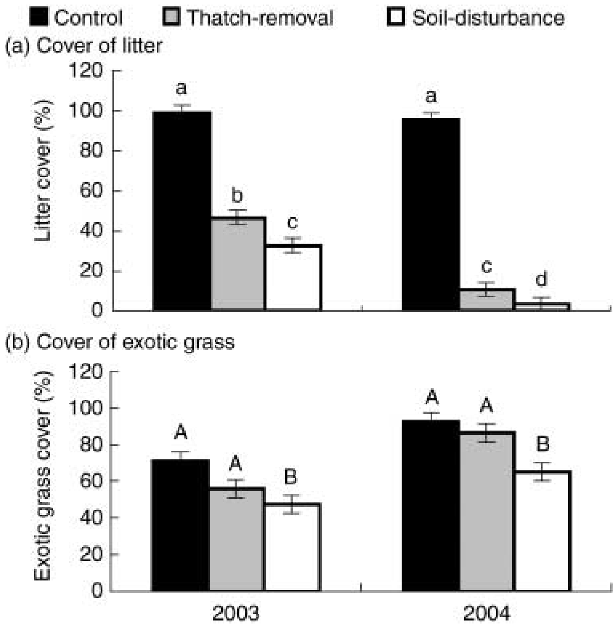

Fig. 4. Soil disturbance experiment: (a) percentage cover of litter and (b) percentage cover of exotic grass in soil-disturbance plots by treatment type in 2003 and 2004 at the Shipley Reserve in Riverside County, California, USA. Uppercase letters indicate significant differences between treatments and lowercase letters indicate significant interaction differences ($P = 0{\cdot}05$). Bars indicate standard error.

Table 3. Grass-control experiment: average species richness per 0·5 m^2 sample in each treatment type in grass-control plots at the Shipley Reserve, Riverside County, California, USA. Numbers in bold type are significantly different from control plots ($P = 0{\cdot}05$). In 1999, herbicide was the only treatment tested. All treatments were tested in subsequent years

Year	Control	Herbicide	Thatch removal + herbicide	Mow
1999	6·1	6·4	0.	0.
2000	5·9	**9·1**	**11·3**	4·2
2001	9·6	10·1	**12·1**	8·5
2002	0·3	**0·8**	**0·8**	0·2
2003	9·6	10·5	**11·4**	9·7
2004	5·8	6·9	6·1	6·0

forbs had up to 60% cover in 2003, compared with about 2% in similar plots during 2004. Likewise, native forbs had up to 40% cover in 2003 but about 6% in 2004. Neither exotic nor native forbs were significantly influenced by thatch removal or soil disturbance during either year.

Discussion

This study supports two models of plant community development for understanding restoration of highly invaded semi-arid shrublands. The first is that a competitive hierarchy (Keddy 1990; Shipley & Keddy 1994) exists in CSS vegetation, with exotic grasses dominant but exotic forbs, particularly species of *Erodium*, moving to dominance as exotic grasses are controlled (Brooks 2000; Allen *et al.* 2005; Prober *et al.* 2005). The resultant competitive hierarchy of grass to *Erodium* plus native forbs demonstrates how little we know about the effects of *Erodium* on emergence and establishment of native species. Although some studies suggest that native species may be less inhibited by *Erodium* than exotic grasses (Gillespie & Allen 2004; Allen *et al.* 2005), Gordon & Rice (1993) found that at least one native perennial species experienced reduced and slowed emergence when grown in the presence of exotic *Erodium*.

Increases in non-native species following removal of an undesirable exotic are known from other ecosystems, such as the removal of *Impatiens glandulifera* that promoted proportionally greater increases in exotic than native species in a riparian system in England (Hulme & Bremner 2005). Post-control increases of secondary exotic species may therefore pose a significant challenge to restoration success. Restoration and management of areas that have multiple invasions must consider how species that are relatively easy to remove, such as grasses, may affect other species that are more difficult to remove, such as *Erodium* spp. However, there may be benefits to increases in some exotic species; at sites such as the Shipley Reserve, where *Erodium* spp. increase as grasses are removed, grass control can have the desirable result of reducing fuels for wildfires, which are also a concern for re-establishment of semi-arid shrublands such as CSS (Cione, Padgett & Allen 2002). In managed systems, the potential impacts of exotic species control must be weighed against benefits such as wildfire reduction.

The second model of plant community development supported by these data is that unpredictable events, such as variable precipitation in semi-arid climates, are as important to community structure as competition from exotic species (Wilson *et al.* 2004; Keeley, Fotheringham & Baer-Keeley 2005). For example, during the very low precipitation year of 2001–02, all categories of plant cover were virtually zero across all treatments. Indeed, cover of exotic grass declined each year from 1999 to 2002 during this period of drought; as precipitation increased during 2003 and 2004, levels of exotic grass cover also increased. Native forb cover also displayed the importance of yearly precipitation levels: 2003 had high forb cover because rains later in the season promote forbs over grasses, not because of treatment effects (Allen *et al.* 2005). Similarly, Keeley, Fotheringham & Baer-Keeley (2005) found that post-fire regeneration of sage scrub at locations near this study is greatly influenced by precipitation patterns, and that the annual components of sage scrub communities are largely dependent on precipitation levels.

Levels and timing of precipitation play a large role in the success of management and restoration efforts (Bakker *et al.* 2003; Hardegree & Van Vactor 2004; Wilson *et al.* 2004; Ogden & Rejmanek 2005). In this study, several treatments altered the community, for example treatments in the grass-control experiment reduced exotic grass cover, and treatments in the soil disturbance experiment reduced litter and increased solar radiation at the soil surface. These treatments, however, did not always increase overall native species cover and did not allow seeded species to establish at the site, at least in part because of the influence of precipitation over these components of the community.

Native forbs and overall species richness did increase in plots that experienced reduced cover of exotic grasses, particularly in plots from which thatch was removed before herbicide was applied, indicating that seed bank limitation (Bekker *et al*. 1997; Bakker & Berendse 1999) is secondary to competitive exclusion in this case. In addition, seeding native species had the effect of increasing the cover of other native forbs that were not included in the seed mix. These effects were probably related; both thatch removal and seeding (as plots were raked prior to seed being broadcast) involved removal of at least some litter. Standing litter, produced primarily by the exotic grasses, is one significant way that Mediterranean grasses alter the characteristics of the communities they invade (D'Antonio & Vitousek 1992; Eliason & Allen 1997; Mack & D'Antonio 1998; Lenz, Moyle-Croft & Facelli 2003). Yearly variation in production and decomposition rate will leave different amounts of litter to affect germinating seedlings in the subsequent growing season. Decomposition of annual grass litter may be 80% to nearly 100% in years of average precipitation (Schimel, Jackson & Firestone 1989; Sirulnik *et al*. 2007), suggesting thatch removal may be justified primarily after years with high production and/or low decomposition in the ecosystem.

The longer term nature of these results provides insight into the community dynamics and challenges to restoration of CSS and other semi-arid ecosystems that have been heavily invaded by exotic grasses and forbs. In such areas, selective grass control may allow other non-native species, particularly forbs, to increase. The strong influence of precipitation on arid and semi-arid communities (Keeley, Fotheringham & Baer-Keeley 2005) further complicates restoration efforts because levels and timing of precipitation may exert a stronger effect on the recruitment and establishment of native species than neighbour effects, at least during extreme years. Restoration and management of such areas will depend greatly on yearly precipitation events, and must be flexible enough to respond to extreme precipitation years.

Exotic grasses present a challenge to the maintenance and restoration of many semi-arid shrub ecosystems (Bush & van Auken 1989; Eliason & Allen 1997; Mack & D'Antonio 1998; Minnich & Dezzani 1998; Cox & Anderson 2004). Grass-control methods, such as herbicides, thatch removal and mowing, can reduce exotic grasses at a site, but grass recovery after a few years indicates they have formed an alternative stable state. Management of these areas for native species may require repeated grass-control efforts. Furthermore, when exotic grasses are controlled, exotic forbs may increase in dominance and inhibit the native community, particularly the shrubs, from fully re-establishing. Because exotic forbs increase when exotic grasses are controlled, management will probably be more successful if it also incorporates efforts to control exotic forbs. However, as exotic forbs are similar in their structure and life cycle to native forbs, controlling them will be more difficult. Control efforts, whether targeting grasses, forbs or both, should be monitored over a longer period, in order to allow long-term effects and climate variability to be understood.

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