Effects of Postfire Grass Seeding on Native Vegetation in Southern California Chaparral

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Abstract

For decades, managers have seeded burned slopes with annual grass in an attempt to increase postfire plant cover and reduce the accelerated hillslope erosion, runoff, and debris flows that typically occur during the first winter after fire. In California, annual ryegrass (*Lolium multiflorum*) was commonly used for this purpose. Critics argue that ryegrass and other seeded grasses suppress native plant regeneration and increase the risk of early reburn. Similar to other researchers, we found that cover of native herbaceous plants was reduced on seeded sites compared to unseeded areas in the first or second year after fire. Density of shrub seedlings was not significantly different between seeded and unseeded plots in our study, but others have found shrub and tree see lings less abundant on seeded sites. In our southern California sites, seeded ryegrass seldom significantly increased plant cover the first growing season after fire, when hillslope erosion was highest. Ryegrass tended to produc greater cover in subsequent postfire years, when native vegetation cover was higher as well. The long-to impact on herbaceous species of suppression by seeded grasses requires further investigation.

Introduction

California's summer-dry climate means that plant moisture content- fuel moisture - is very low by late summer and conditions are right for fire. Where fuel accumulation has become unnaturally high, is in many conifer stands, or where chaparral is the dominant plant cover, fires can bum with high intensity and severe fire effects. Stand-replacement fires remove vegetation cover from large areas and expose soil to rain, wind, and the force of gravity. During the first winter after fire, rain storms of even moderate intensity can mobilize destabilized hillslope surface material and cause major downstream debris flows and flooding (Wells 1987). If downslope values are at risk from increased sedimentation and runoff, or where retaining soil productivity is a priority, agencies such as the USDA Forest Service and California Department of Forestry implement postfire emergency watershed rehabilitation. One of the most common emergency rehabilitation methods is the application of grass seed to burned slopes to increase plant cover and hold soil in place. Non-native annual grasses are typically used for this purpose because they germinate quickly, grow aggressively, form extensive fibrous root systems, are relatively cheap, and can easily be applied from the air. The practice has stirred considerable controversy, however.

In California, annual ryegrass (*Lolium multiflorum* Lam.) has been used extensively for postfire seeding (Barro and Conard 1987). Critics of grass seeding point to evidence that ryegrass suppresses the native postfire herbaceous flora (Keeley et al. 1981, Nadkarni and Odion 1986, Taskey et al. 1989), can outcompete shrub or tree seedlings (Schultz et al. 1955, Griffin 1982, Conard et al. 1991), may create flashy fuel conditions conducive to an early reburn that can alter vegetation composition (Zedler et al. 1983), and has not been rigorously demonstrated to effectively reduce erosion during the first winter after fire, especially in southern California (Conrad 1979, Taskey et al. 1989). Defenders cite arguments that even small reductions in hillslope erosion due to ryegrass seeding justify the method's relatively low cost (Rice et al. 1965, Miles et al. 1989) and the political necessity to do something after fire because the public has come to expect it (Arndt 1979, Gibbons 1995).

Although some monitoring of postfire rehabilitation projects has been done and considerable experiential knowledge exists, rigorous quantification of seeding effects has been lacking (Barro and Conard 1987). Studies have suffered from inadequate sample sizes (Blankenbaker and Ryan 1985), lacked true unseeded "control" plots against which to compare seeded areas (Orr 1970, Griffin 1982, Conard et al. 1991), experienced severe animal disturbance on small plots

(Taskey et al. 1989), or were confounded by extremely low precipitation the first winter after fire (Rice et al. 1965). Many efforts to monitor postfire seeding success remain unpublished.

Much of the concern over seeding has focused on chaparral ecosystems, in which a specialized postfire annual plant flora takes advantage of the light, space and soil nutrients available after fire and some of the dominant shrub species recover from fire only from, seed (Sampson 1944, Sweeney 1956, Keeley et al. 1981). Competition from seeded grasses could reduce populations of postfire annuals during their "window of opportunity" after fire, leading to decreased seed production and a smaller seed bank in the soil awaiting the next fire. Reduction in survival of shrub seedlings because of grass competition could produce a shift in plant community composition to dominance by species that survive fire and resprout.

To address some of the limitations of previous investigations, in 1986 we initiated field experiments to evaluate the impacts of postfire ryegrass seeding on hillslope erosion and chaparral plant community recovery. Our experimental design included replication of study sites over four regions within coastal southern California and a large number of plots within each site. By using prescribed fires rather than setting up plots opportunistically after wildfires (as in previous studies), we were able to compare postfire erosion and vegetation composition to prefire values on the same sites. We also monitored sites for up to 5 years after fire, far longer than most previous studies. This paper presents vegetation data collected in the study; a companion paper (Wohlgemuth et al., this volume) reports the erosion results. We were also able to look for residual effects of ryegrass seeding on the postfire herbaceous flora of one site which reburned in a wildfire 5 years after the original prescribed fire.

Methods

Chaparral Ryegrass Seeding Study. Study sites were established in areas of mature, mixed chaparral scheduled to be burned in high-intensity prescribed fires by federal, state or county agencies as part of their fuel hazard reduction programs. Although nine study sites were installed, only four were eventually burned in management fires. They were located in separate coastal mountain ranges and burned in different years (Figure 1; Table 1). Sites were given the name of the bum project or a nearby landmark. An additional study site, Belmar2, was created by a wildfire in November 1993; it consisted of previously unburned plots from the Belmar study site, the rest of which was burned 5 years earlier (1988) in a prescribed fire.

At each site, 60 unbordered erosion plots (Wohlgemuth et al., *this volume)* and 40 2-m by 10-m vegetation plots were installed before the fire. Prefire vegetation measurements included shrub density and cover by species. After the fire on each site, fire severity was evaluated on each plot and only those plots where severity was moderate or high (definitions in Table 1) were retained in the study (from 20 to 38 of the original 40 vegetation plots, depending on site; Table 2). In the fall after each fire, half of the retained plots were randomly chosen to be seeded with annual ryegrass. Seed was applied by hand with rotary fertilizer spreaders at a target rate of 430 seeds m^{-2} (40 seeds ft^{-2}), which is equivalent to 9 kg ha^{-1}(8 lb ac^{-1}), a common rate used in aerial seeding. Seed was tested for germination before use, and seeding rate was monitored using sticky papers on site.

Vegetation development on seeded and unseeded plots was measured each spring when herbaceous species were at peak biomass, for up to five years after fire. To facilitate cover determination, each plot was divided into five 2-m by 2-m subplots. Percent cover of each species present was estimated in each subplot by inspection (most years) or by the number of centimeters each species intercepted along a 2-m line through the subplot (1991 and 1992 at Belmar, Bedford and Vierra) (Oosting 1958). Plot cover was averaged from the five subplots. Trace species were assigned a cover value of 0.01%. Shrub seedlings were counted within five randomly-chosen 1-m by 1-m subplots in each plot. The canopy volume of each sprouting shrub within each plot was estimated by measuring the shrub's height and two canopy diameters, simply treating each shrub as a cube. Differences in vegetation variables between seeded and unseeded plots were analyzed using a two-sample randomization test (Manly 1991). Each p-value was estimated from 1,000 randomizations, and only p-values less than 0.05 were considered significant.

Residual Effects of Ryegrass Seeding. One of the ryegrass seeding study sites, Belmar, was reburned in a Santa Ana wind-driven wildfire five years after the original prescribed fire (the same fire that created the Belmar2 site). Postfire vegetation development was monitored each spring at this "Belmar Reburn" site in the manner described above. To evaluate possible residual impacts of grass seeding on species dependent on fire for survival ("fire followers"), a group of herbaceous species commonly found after fire were analyzed separately. Cover of these species on previously seeded and unseeded plots was compared using the two-sample randomization test.

Results

Chaparral Ryegrass Seeding Study. Most of the study sites burned in summer or fall (Table 1) and were seeded in the fall before winter rains began. The Buckhorn fire was conducted in early March 1994, toward the end of the rainy season, and seeding was not done until the following fall. Although vegetation sampling was conducted at Buckhorn in late spring of 1994 (1994 columns on Figure 2), the spring of 1995 is considered the fist growing season after fn for the purpose of comparing seeded to unseeded treatments on that site.

At the end of the first growing season after fire and seeding, total vegetation cover was not significantly different (p>0.05) between seeded and unseeded plots at any site except Vierra (burned November 1990). At Vierra, vegetation cover was extremely low even on the ryegrass-seeded plots and consisted mostly of sprouting shrubs (Figure 2). At Belmar and Buckhorn, cover of herbaceous species other than ryegrass was significantly less (p<0.05) on seeded plots during the fist year; there was no difference at the other sites. Ryegrass achieved its maximum absolute cover during the fist growing season at Belmar and Buckhorn, declining in subsequent years.

In the second and third postfire growing seasons, total vegetation cover again was significantly greater on seeded plots only at Vierra (Figure 2). Ryegrass cover on seeded plots was greatest during the second growing season after fire at Bedford, Vierra, and Belmar2. Cover of herbaceous species other than ryegrass was significantly lower on seeded plots than on unseeded plots during the second growing season after fire on these sites as well (Figure 2). Ryegrass cover decreased at all sites (for which we have data so far) in the fourth and fifth growing seasons after fire, and there were no significant differences in cover between seeded and unseeded plots (data not shown).

Sprouting shrub canopy volume and total shrub cover were not significantly different between seeded and unseeded plots at any site (p> 0.05; data not shown). At all sites except Bedford, a species of *Ceanothus* that is killed by fire and must regenerate from seed was an important component of the prefire shrub vegetation (Table 1; *C. megacarpus* at Belmar and Belmar2; C. *cuneatus* at Vierra and Buckhorn). *Ceanothus* seedling densities in seeded and unseeded plots were not significantly different (p>0.05) at any site during the first three growing seasons after fire (Table 2). At all sites, density of surviving *Ceanothus* seedlings decreased over the years, but after 3 to 5 years it was still greater than prefire shrub density.

Residual Efects of Ryegrass Seeding. On the Belmar Reburn site, the combined cover of 10 postfire annual and perennial "fire follower" species was not significantly different (p>0.05) between plots that had previously been seeded and those that had not during the fist two years after the site reburn (Table 3). Total herbaceous plant cover was higher on the Belmar Rebum plots each year than on Belmar2, primarily due to high cover by non-native species such as *Bromus madritensis* (red brome) and *Hirschfeldia incana* (shortpod mustard). These weedy naturalized exotics were uncommon at both Belmar (prescribed burn) and Belmar2 the fist year after fire, but they increased in abundance during the second growing season at Belmar (Table 3). Brome and mustard had achieved high cover by the fifth year after the prescribed fire at Belmar (Beyers et al. 1994).

Discussion

Chaparral stands have a soil "seed bank" of shrub and herbaceous species, many of which are stimulated to germinate by heat, smoke, or chemicals leached by rain from burned wood (Keeley 1991, Keeley and Fotheringham 1997). Seedlings appear during the fist spring after fire. Annual grasses are sown onto burned chaparral sites to increase plant cover when the soil seed bank is believed to have been destroyed or is thought to be inadequate to provide timely watershed protection (Brown 1995, Wickizer 1995).

Ryegrass seeding did not increase total plant cover during the fist growing season after fire on most of our sites. Only on the site with the least herbaceous vegetation cover -- Vierra -- did ryegrass-seeded plots have significantly greater total average plant cover than unseeded plots, but cover was very low in both cases. The slightly greater plant cover was not associated with a significant decrease in winter erosion the first year after fire (Wohlgemuth et al., *this volume).* We do not know if the low first-year herbaceous cover was due to a naturally small soil seed bank, a particularly hot fire, or the uneven distribution of rainfall in 1990-1991-the first winter after fire for Vierra, when most of the season's rain fell in March (Conard et al. 1995). Ryegrass-seeded plots continued to have higher total vegetation cover than unseeded plots in the second and third growing season at Vierra, though by the third year most plant cover consisted of shrubs (primarily sprouted chamise).

Keeley et al. (1981) observed a negative relationship between ryegrass cover and cover of native fire-adapted annual plants in their study of several sites in San Diego County. We also found that annual ryegrass tended to replace, rather than supplement, natural herbaceous plant cover. Our results are similar to other postburn studies in southern California chaparral (Gautier 1.983, Nadkarni and Odion 1986, Taskey et al. 1989). Cover of native herbaceous vegetation, particularly fire-followers, was lower on seeded plots than on unseeded plots in years when ryegrass cover was highest, and species richness was lower on seeded plots as well (Beyers et al. 1994).

The long-term impact of the reduction in postfire native herbaceous plant cover and species richness on ryegrass-seeded sites is unknown. Observers have long noted that certain annual and perennial plant species germinate and grow almost exclusively in the first growing season after a fire (Sampson 1944, Sweeney 1956, Keeley et al. 1981). Reduction in populations of these postfire specialists might reduce the seed bank available to germinate after the next fire (Conard et al. 1995). In this study, although we observed lower cover of native herbaceous plants on seeded plots compared to unseeded plots during the critical first year after the prescribed fire at the Belmar site, we found no residual difference in the cover of at least the most common native herbaceous species after a wildfire reburned the site five years later. This may be partially explained by the great reduction in ryegrass cover that occurred during the second, extremely dry growing season at Belmar (Beyers et al. 1994, Wohlgemuth et al. *this volume)* and the concomitant increase in cover by native species, allowing them to contribute to the soil seed bank. Less common native species were too infrequent to allow analysis, so we could not assess the long-term impacts of grass-seeding on rare species. Many postfire herbaceous species persist into the second year after fire, when ryegrass cover is usually greatest and negative impacts on native plant reproduction might be greater. Resampling formerly seeded and unseeded plots after future wildfires, on sites where ryegrass cover was relatively high for several years, will greatly increase our understanding of the residual effect of ryegrass suppression on native chaparral herbs.

Unlike herbaceous cover, shrub seedling density was statistically unaffected by ryegrass seeding. On the four sites with prefire populations of *Ceanothus* species that are killed by fine, density of *Ceanothus* seedlings was not significantly different on seeded and unseeded plots (though first-year density tended to be lower on the Belmar site, with p=0.07). Shrub seedling density after 3 to 5 years appeared sufficient to replace plants killed by fire, although more *Ceanothus* mortality may be expected in later years as stands develop and plant competition increases (Riggan et al. 1988). Average ryegrass cover during the first winter after fire, when shrub seedlings germinate and become established, did not exceed 20% on any of our study sites, even though total first winter precipitation ranged from 389 to 1105 mm (15.3 to 43.5 inches) at the various sites (Wohlgemuth et al. *this volume).* As noted, most sites had no difference in total herbaceous cover between seeded and unseeded plots. Conard et al. (1995) suggested that total herbaceous cover may be more important than species composition in its impact on shrub seedling density. Where winter and spring conditions result in high grass cover (> 40%) during the first growing season after fire, as in northern California, shrub seedlings may be suppressed by seeding (Schultz et al. 1955, Conard et al. 1991).

From our study and others, it appears that ryegrass seeding does not reliably increase total plant cover on burned chaparral slopes, at least in southern California, and that it grows at the expense of the native herbaceous flora. However, much postfire grass seeding occurs in forested areas, where maintenance of site productivity as well as protection of other resources are goals of postfire seeding. There is relatively little published information available on the impacts of grass seeding on native vegetation recovery in the conifer zone.

Orr (1970) examined plant cover and erosion after fire in the Black Hills of South Dakota, concluding that seeded species were essential to the recovery of hillslope stability. He did not include any unseeded sites in his study, however. The impact of the seeded grass and legume species on native plant regeneration was not examined directly, but his vegetation graphs show that on one site, native cover was lower on plots with "dense" cover of seeded grasses compared to those with "sparse" cover, particularly in the second to fourth year after fire. At the other site, cover of both native vegetation and seeded species tended to be higher on the "dense" plots, suggesting site quality differences between the two sampling areas.

In Idaho, Geier-Hayes (1997) found that plots seeded with non-native grasses had lower native vegetation cover than unseeded plots for up to five years after fire, even though seeded grass cover had declined in later years. Total plant cover, including seeded and native species, did not differ between seeded and unseeded plots in any of the three forest types examined.

In one of few studies from a forested area in California, Janicki (1989, unpublished) reported first-year monitoring results from the 1987 Stanislaus Complex Fire seeding effort. He found a wide range of ryegrass cover on the 29 seeded plots sampled, from 2% to 92%, with only half of the plots having total plant cover exceeding 30%, which he considered a minimum necessary to affect erosion. Compared to the 12 plots in unseeded areas, ryegrass-seeded plots had greater plant cover on average but it seemed to come at the expense of native vegetation (Janicki 1989). Although stating that the unseeded areas sampled were similar physically to the seeded areas, the report includes photos which show chaparral type vegetation remains in "unseeded" plots compared to pine remains in "seeded" plots, a difference that complicates interpretation. Janicki also found that ryegrass cover was significantly associated with percent slope: plots with greater than 30% ryegrass cover were found predominantly on slopes of less than 35%. Some of the grass seed apparently washed off steeper slopes with the first rains (Janicki 1989). Conard et al. (1991) sampled 75 vegetation plots on ponderosa pine sites during the second year after the Stanislaus Complex Fire. The plots encompassed a range of site conditions and grass densities, but included no unseeded areas primarily because they couldn't locate any with similar prefire vegetation. Pine and shrub seedling densities and native herbaceous plant cover were lower on plots where average ryegrass cover exceeded 40% (Conard et al. 1991).

These results suggest that "successful" seeding operations will always result in some suppression of natural herbaceous regeneration. Whether that suppression will affect long-term herbaceous plant population viability is unknown. Prudence suggests that managers should avoid seeding areas of known rare plant occurrence, and this has become standard practice in most seeding operations in recent years. The negative effect of high grass cover, either seeded or natural, on conifer seedling growth and survival has been known to foresters for years (Baron 1962, Larson and Schubert 1969, Stewart and Beebe 1974). However, tree seedlings might benefit if they are planted after seeded grasses suppress competing shrub seedlings (Conard et al. 1991), provided the grass can be controlled.

Agencies such as the USDA Forest Service and California Department of Forestry and Fire Protection are required by law to mitigate emergency watershed conditions caused by wildfire (Brown 1995, Wickizer 1995). Protection of human life and property are paramount. Seeding has been justified, despite its known negative impacts on native vegetation, because the emergency condition it seeks to remedy overrides the ecological concerns (Brown 1995, Wickizer 1995). However, because many studies have found that seeded grasses do not increase total plant cover, particularly on chaparral sites, during the first year after fire when the threat of increased erosion and sedimentation is greatest, more quantification of the impact of grass seeding on erosion is essential. Controlled studies and well-designed monitoring efforts are needed to compare the benefits of postfire seeding for erosion control against the ecological and economic costs.

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Table 1. Characteristics of five chaparral study sites in coastal southern California. Slope and shrub cover values are means ± s.e.

	Bedford	Belmar	Belmar2	Buckhorn
Mountain Range	Santa Ana	Santa Monica	Santa Monica	Santa Ynez
Elevation (m)	670	450	450	1035
Mean Aspect	NE	S	SSE	SSW
Mean Slope ()	36 ± 0.8	27 ± 0.9	27 ± 0.8	33 ± 0.7
Prefire Live Shrub Cover (%)	33 ± 1.7	45 ± 4.3	48 ± 2.7	28 ± 3.3
Dominant Prefire Shrub Species	*Quercus berberidifolia* *Prunus ilicifolia* *Rhamnus ilicifolia* *Fraxinus*	*Ceanothus megacarpus* *Malosma laurina* *Cercocarpus betuloides* *Heteromeles*	*Ceanothus megacarpus* *Malosma laurina* *Cercocarpus betuloides* *Heteromeles*	*Ceanothus cuneatus* *Adenostoma fasciculatum* *Quercus berberidifolia* *Prunus*
Burn Month/Year	July 1990	June 1988	Nov. 1993[1]	Mar. 1994
Fire Severity[2]	High	Moderate	High	High

[1] Burned in wildfire; other sites burned in prescribed fires.
[2] Moderate severity: leaf litter mostly consumed; soil charred to 1 cm depth; >25% unburned foliage remaining. High severity: leaf litter completely consumed; soil charred to 2.5 cm depth; foliage completely consumed.

Table 2. Mean prefire density (number m^{-2} ± s.e.) of shrubs of *Ceanothus* species which are killed by fire at four study sites, and mean postfire densities of seedlings of those species in seeded and unseeded plots.

	Belmar		Belmar2		Buckhorn		Vierra	
	Unseeded (n = 10)	Seeded (n = 10)	Unseeded (n = 14)	Seeded (n = 14)	Unseeded (n = 11)	Seeded (n = 13)	Unseeded (n = 19)	Seeded (n = 19)
Prefire # m^{-2}	0.3 ± 0.15	0.2 ± 0.09	0.4 ± 0.09	0.4 ± 0.10	0.3 ± 0.03	0.5 ± 0.08	0.4 ± 0.06	0.3 ± 0.05
Postfire # m^{-2}								
Year 1	4.6 + 1.4	1.7 ± 1.0	9.4 ± 3.4	6.6 ± 3.2	6.9 ± 1.7	4.2 ± 1.3	5.4 ± 0.9	5.6 ± 1.0
Year 2	0.4 ± 0.2	0.2 ± 0.2	2.9 ± 0.9	2.3 ± 0.7	0.7 ± 0.3	0.4 ± 0.2	3.9 ± 0.7	3.4 ± 0.8
Year 3	0.4 + 0.2	0.4 ± 0.2	2.2 ± 0.7	1.7 ± 1.7	0.6 ± 0.3	0.4 ± 0.2	2.0 ± 0.4	2.0 ± 0.4

Table 3. Percent cover (± s.e.) of "fire follower" annual and perennial herbaceous species and other herbaceous vegetation categories on the Belmar prescribed fire, Belmar reburn, and Belmar2 wildfire sites during the first and second growing seasons after fire. Unseeded values followed by an asterisk (*) are significantly different from seeded values at p<0.05.

	Belmar Prescribed Fire		Belmar Reburn		Belmar2 Wildfire	
	Unseeded	Seeded	Previously Unseeded	Previously Seeded	Unseeded	Seeded
Year 1(n = 10)	(n = 10)	(n = 10)	(n = 10)	(n = 14)	(n = 14)	
"Fire Followers"[1]	24.1 ± 4.3*	6.7 ± 1.7	20.7 ± 4.1	27.1 ± 5.1	19.7 ± 3.3	12.7 ± 4.1
Ryegrass	0	12.4 ± 2.0	0	0	0	6.6 ± 2.0
Biome and Mustard[2]	0.2 ± 0.2	0.6 ± 0.4	18.6 ± 5.9	36.1 ± 4.1	4.5 ± 1.5	1.7 ± 0.7
Total Herbaceous[3]	30.6 ± 4.8	21.4 ± 2.1	63.6 ± 6.4	75.8 ± 6.2	31.4 ± 5.1	28.6 ± 7.4
Year 2						
"Fire Followers"[1]	30.0 ± 3.0	26.8 ± 3.5	35.2 ± 6.8	26.4 ± 5.6	66.9 ± 5.1*	43.8 ± 5.6
Ryegrass	0	3.2 ± 1.4	0	0	3.3 ± 1.4	29.8 ± 7.6
Brome and Mustard[2]	1.2 ± 0.8	3.6 ± 2.2	49.8 ± 9.6	75.7 ± 5.6	0.7 ± 0.3	0.4 ± 0.2
Total Herbaceous[3]	40.2±4.6	37.1±4.7	121.4±12.3	141.5±7.0	97.0±6.0	87.7±7.4

[1]"Fire Followers" = *Phacelia distans* (caterpillar phacelia), P. *cicutaria* (caterpillar phacelia), *P. grandiflora* (large-flowered phacelia), *P. viscida* (sticky phacelia), *Calystegia macrostegia* (wild morninglory), *Cryptantha* spp. (popcorn flower), *Mentzelia micrantha* (stickleaf), *Lotus salsuginosus*, *Emmenanthe perduliora* (whispering bells), and *Eucrypta chrysanthemifolia* (eucrypta).

[2] Brome and Mustard = *Bromus madritensis* (red brome) and *Hirschfeldia incana* (shortpod mustard), two introduced (non-native) weedy species.

[3] Total Herbaceous - sum of covers of all individual herbaceous species, including ryegrass. Plant canopies overlapped so total cover can exceed 100%.

Figure 1. Location of chaparral sites used in this study. Each site is located in a coastal mountain range.

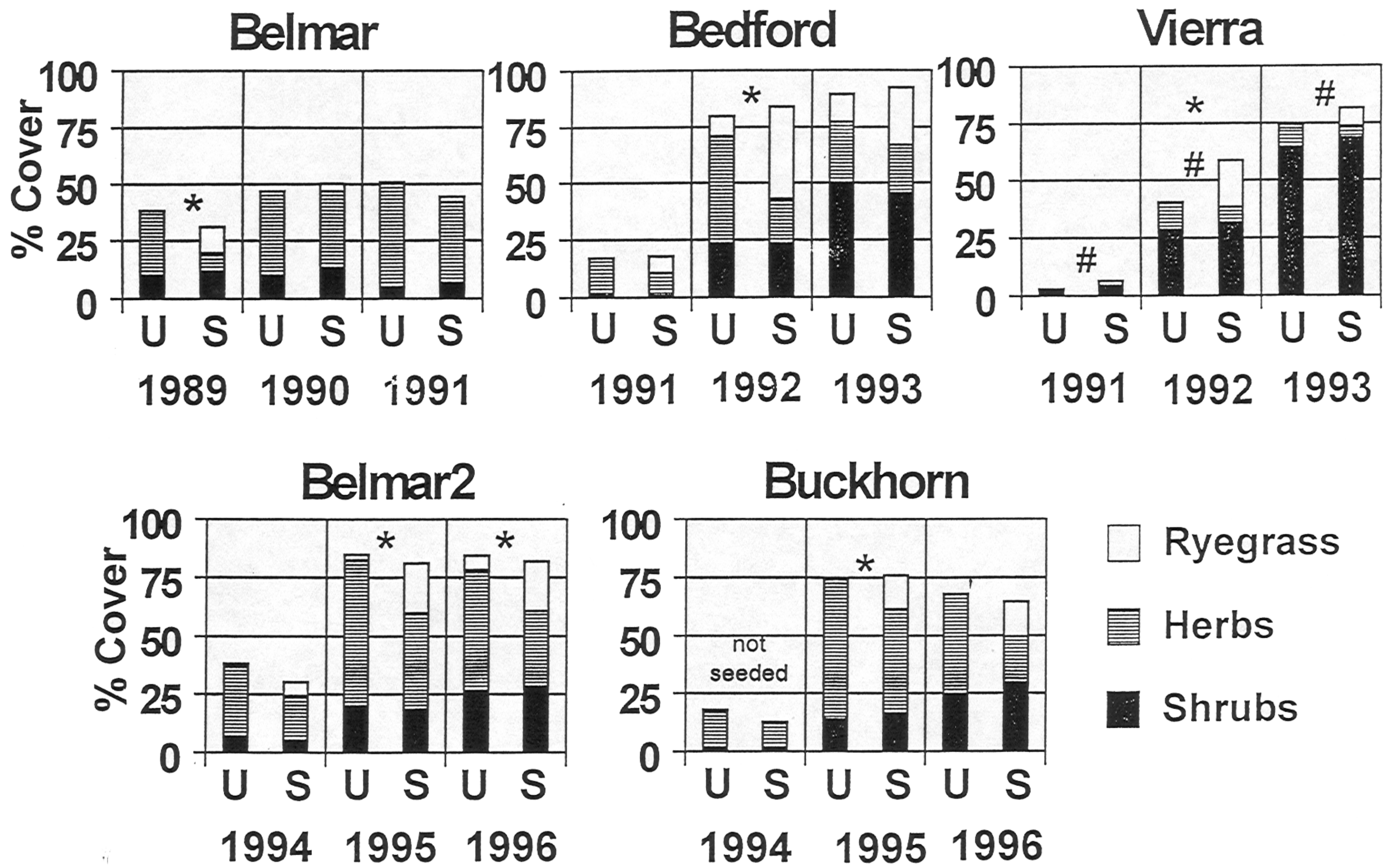

Figure 2. Mean total vegetation cover at five chaparral study sites, measured in late spring during the first hree growing seasons after fire. Bars are divided into relative mounts of shrub, herbaceous, and ryegrass cover (actuval cover of individual species added to more than 100% in some years). Within each year: U = unseeded plots; S = seeded plots; # = mean total cover significantly difference between seeded and unseeded plots at $p < 0.05$; * = mean herbaceous cover other than ryegrass significantly different between seeded and unseeded plots at $p < 0.05$.