Restoration of *Artemisia* Shrublands Invaded by Exotic Annual *Bromus*: A Comparison Between Southern California and the Intermountain Region

Edith B. Allen

Abstract: Sagebrush shrublands of southern California and the Great Basin are both undergoing massive vegetation-type conversion to exotic annual grasslands dominated by brome species. In southern California the main players are California sagebrush and red brome, while the Intermountain Region has big sagebrush and cheatgrass. Exotic annuals tend to be more dominant in soils with moderate to high levels of soil P and N. The type conversion of California sagebrush shrublands has been occurring during the last 25 to 30 years, compared to the last 100 years in the Great Basin. One reason for this might be the recent increase in anthropogenic N deposition caused by automobile emissions, up to 30 kg N per ha year. Field fertilization experiments in southern California also showed the exotic annual grasses have increased biomass with elevated N. The increased grass biomass has likely fueled more frequent fires in California. Even though California shrublands are adapted to fire compared to the big sagebrush-grasslands, frequent fire inhibits the re-establishment of shrubs when brome and other annual grasses are abundant. Restoration attempts have included timed fire to deplete the annual seedbank, herbicides, mowing, grazing, and reseeding and replanting. A comparison of some of these restoration efforts will be done for the two regions.

Introduction

The invasion of exotic annual grasses into native vegetation has been proceeding in some areas of the world for the last 100 years (D'Antonio and Vitousek 1992), and is currently affecting two major regions of the United States. The invasion of cheatgrass (*Bromus tectorum*) into big sagebrush (*Artemisia tridentata*) shrub-grasslands of the Intermountain Region is by now well documented (Mack 1981; McArthur and others 1990; Monsen and Kitchen 1994), although few large-scale solutions to restore native species have been implemented (Pellant 1994). A parallel but more recent invasion is occurring with the invasion of red brome (*Bromus madritensis* ssp. *rubens*) and other species of brome grasses, wild oats (*Avena*), barley (*Hordeum*), and annual fescues (*Vulpia*) into California sagebrush (*Artemisia californica*) shrublands of the coastal sage scrub vegetation of California. The latter invasion is so recent, an event that has been occurring over the past 25 to 30 years, that there is still little awareness that it is even occurring, or that it represents a permanent shift in vegetation type from perennial shrubland to annual grassland (Allen and others 1998; Minnich and Dezzani 1998). Yet this invasion has such similarities with the better-studied cheatgrass invasion that the parallel cannot be missed. Through a comparative examination we can learn lessons from cheatgrass invasion that may be applied to California sagebrush invaded by annual brome and other grasses, both what to expect and what control and restoration measures may be implemented. The objective of this review is to examine the similarities and differences of the two invasions by examining the ecology of the species, the climates, soils and disturbance regimes of the two regions. I will discuss potential reasons for the recent invasion and vegetation-type conversion of California sagebrush, and the potential for restoration of this vegetation as compared to big sagebrush.

Land Area Affected and Site Descriptions

California sagebrush is one of several dominant shrubs of the coastal sage scrub (CSS) vegetation that extends along the coast from the San Francisco Bay area southward into Baja California. The vegetation has its greatest extent and inland distribution in southern California in Riverside County and adjacent counties, where it is called inland sage scrub or Riversidean sage scrub (Westman 1981). The more inclusive term CSS will be used to include those areas codominated by such species as California buckwheat (*Eriogonum fasciculatum*) and brittlebush (*Encelia farinosa*) that are also undergoing conversion to exotic annual grasslands.

The CSS of southern California is among the most intensively human-impacted vegetation types in the United States. For this reason it has become a focus for mitigation and restoration (Bowler 1990), driven by the legal requirements

In: Hild, Ann L.; Shaw, Nancy L.; Meyer, Susan E.; Booth, D. Terrance; McArthur, E. Durant, comps. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12–16; Laramie, WY. Proceedings RMRS-P-31. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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of the Endangered Species Act (ESA). Currently, Habitat Conservation Plans under the ESA are underway in a number of counties of southern California that have large components of potential CSS, some with up to 160 threatened, endangered, and sensitive species (http://www.ecoregion.ucr.edu). CSS has been subject to urbanization, agriculture, and invasion by exotic annuals to such a large extent that one estimate gives only 10 percent of the original vegetation in good condition (Westman 1981). A more recent estimate puts CSS loss at 66 percent (O'Leary and others 1992), but in either case it is a significant loss because CSS covers only about 1.2 million ha of land area. The difference between the estimates may lie in the inability to estimate accurately how much of the natural potential vegetation is CSS, and it may lie in the condition of the remaining vegetation, which is often very weedy. Large expanses of CSS have been invaded by Mediterranean annual grasses and forbs (Freudenberger and others 1987), and in many areas the shrub understory is dominated by exotic rather than native annuals (Minnich and Dezzani 1998; Stylinski and Allen 1999). The conversion of shrubland to Mediterranean annual grassland has occurred primarily in the last 25 to 30 years, with 90 percent loss in shrub cover close to urban areas in western Riverside County and permanent replacement by annual grasses (Minnich and Dezzani 1998). Exotic annual grasses invaded California native grasslands over the past 200 years (Heady 1977), but the vegetation type-conversion of CSS to exotic annual grassland is a recent phenomenon.

The big sagebrush-grasslands of the Great Basin, the Columbia Plateau, and the Colorado Plateau have been undergoing invasion of cheatgrass and other species for more than 100 years (Billings 1990; Mack 1981; Young and others 1972). I will rely on literature citations and use less detail in explaining the cheatgrass conversion, as it is better documented than the California situation, and was the subject of two earlier Shrub Symposium volumes (McArthur and others 1990; Monsen and Kitchen 1994). Some 18 million acres of Intermountain rangeland have been invaded by cheatgrass plus medusahead (Pellant and Hall 1994). In fact, cheatgrass is still invading new areas where it has been sparse or absent, as in shrub-grasslands of the Colorado Plateau in Utah (Gelbard and Belnap 2003).

The big sagebrush type-conversion does not have the extensive conservation implications for endangered species as does the CSS. There are, however, several notable restoration projects for endangered animals such as the black-footed ferret and the sage grouse (Wrobleski and Kauffmann 2003; Wirth and Pyke 2003) in the big sagebrush-grasslands, as well as some endangered plant species such as *Silene spaldingii* in Montana (Lesica 1997) and *Gaura neomexicana* subsp. *coloradensis* in Wyoming (Munk and others 2002). However, huge land areas of big sagebrush are involved relative to the California CSS, and although certain species are of concern, the area does not have the hundreds of sensitive species that California has. This fact has implications for policy on restoration, which is driven by mitigation coupled with development in California, while restoration is more often driven by land productivity needs in the big sagebrush-grassland regions.

Climate and Phenology

Cheatgrass and the Mediterranean grasses occur in semi-arid, winter-wet, and summer-dry climates, but cheatgrass occurs in areas with winter frost, while the Mediterranean grasses are frost intolerant. Their precipitation regimes are broadly overlapping, although red brome also occurs in cool and/or less dry desert areas. Cheatgrass typically germinates in the fall in areas where few or no native species are adapted as winter annuals, as it has frost-tolerant seedlings. Cheatgrass is not persistent in the eastern edge of big sagebrush-grassland where summer rains are more frequent than in the Great Basin. Warm season grasses make their appearance in regions with summer rain, and winter annuals cannot compete. In addition, the high basins and high plains of regions to the east of the Great Basin have cold winters that are not conducive to the survival of winter annuals. In the sagebrush-grassland (1,500 m) of eastern Wyoming, cheatgrass is a spring annual in most years that senesces by early summer (Allen and Knight 1984).

The Mediterranean annual grasses also germinate with the onset of fall rains, and are often phenologically earlier than California native annuals and perennials (Chiariello 1989). The earlier phenology makes the exotic grasses highly competitive with native species. Plant growth occurs during the mild and rainy winter growing season in California, as summers are dry. The following spring the grasses produce seeds and senesce at the same time or earlier than native annuals. In the Mediterranean, rainfall typically continues later into the spring and early summer, giving an advantage to native perennial species that persist into the dry summer. Annual grasslands are considered early successional in the Mediterranean, and the extent of annual grasslands is less than in California (Jackson and Roy 1989). The annual grass phenology coupled with the shorter rainfall season is cited as the reason for persistence of the annual grasslands in California (Jackson and Roy 1989). Another argument is made below that soils may also contribute to the dominance of Mediterranean grasses in California.

Soil Nitrogen and Phosphorus

Soil nutrients may also contribute to the abundance of exotic annual grasslands in the Western United States. The Mediterranean has primarily calcareous soils originating from marine limestone deposits (Blondel and Aronson 1999), while much of southern California has granitic soils (Norris and Webb 1976). Both regions have volcanic outcroppings, more extensive in northern California. The calcareous soils of the Mediterranean are phosphorus fixing, with low extractable levels of P (Rabinovitch-Vin 1983). Grasslands dominate in volcanic outcroppings that have higher levels of soil P, but not in calcareous soils. For instance, the region around the Sea of Galilee in Northern Israel is volcanic with an annual grassland, while nearby calcareous soils are dominated by Mediterranean shrublands (Rabinovitch-Vin 1983). The soils of southern California tend to have moderate to high P levels. Measured amounts in sites in San Diego and Riverside Counties were 20 to 40 mg per kg bicarbonate extractable P, and 700 to 1,000 mg per kg total P (Cannon

and others 1995; Nelson and Allen 1993; Padgett and others 1999).

Not only soils of southern California, but also much of the Great Basin are relatively high in extractable P. A survey of soil P from 90 locations across the Western United States where big sagebrush (*A. tridentata* ssp. *tridentata*) occurs, showed that most of the sites had levels of P from 11 to 20 mg per kg, with a mean of 15.3 (S.E. = 0.9). The exceptions were sites on the edges of its distribution, such as North Dakota and Baja California, that had under 10 mg per kg (fig. 1). This indicates that big sagebrush is a species of moderate to high P soils, but may also explain why it is so invasible by exotic species that have their greatest extent in soils rich in P in their home environment. Many invasive species have agricultural origins, either from cropland or pasture, and may be well adapted to soils naturally rich in nutrients.

Some Great Basin soils are also relatively high in N, and cheatgrass is highly responsive to N fertilizer (for example, Yoder and Caldwell 2002). The soils of southwest Wyoming sagebrush-grassland had 6 percent organic matter and 0.5 percent total Kjeldahl N, a surprisingly high amount for a semiarid soil (Waaland and Allen 1985). The richness of these soils may be explained by their geologic history. Some are relicts of more mesic vegetation from the last glaciation, while others are in sedimentary basins that in some cases were Pleistocene lake bottoms (Fiero 1986). Exotic plant invasion was highly correlated to soils high in P and N in southern Utah (Bashkin and others 2003).

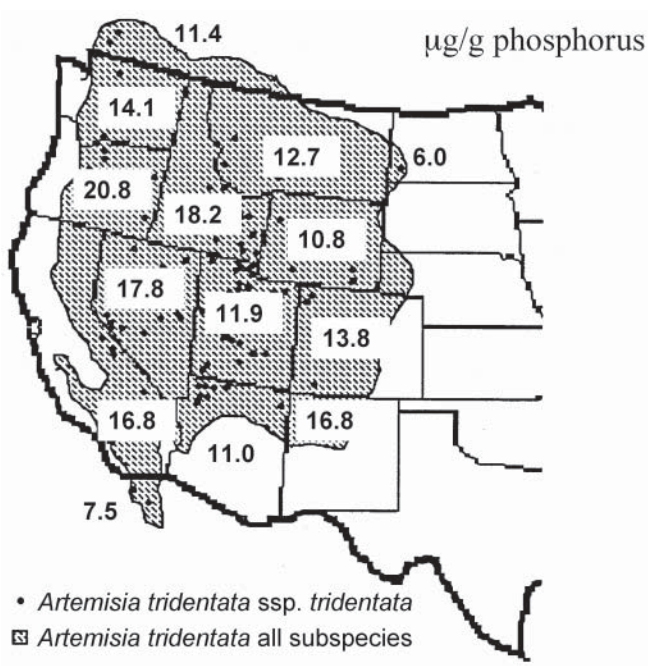

Figure 1—Concentrations of bicarbonate extractable soil P in sites dominated by *Artemisia tridentata* ssp. *tridentata* (data from E. Allen and M. Allen).

Nitrogen Deposition as a Cause of Invasion

The relatively high soil nutrient levels may explain in part why annual brome grasses have invaded big sagebrush-dominated lands of the Intermountain Region in the past, but not why the CSS of California has been recently invaded. The urbanizing areas of southern California are also subject to anthropogenic nitrogen deposition, which has been occurring for the past 40 years primarily as NOx from automobile emissions (fig. 2). The adoption of the catalytic converter in the mid-1980s caused a general decline in emissions, but NOx is still high enough to cause elevated soil N (Padgett and others 1999). NOx is converted to the plant-available forms of HNO_3 per NO_3^- in the atmosphere. In agricultural regions, NH_3 per NH_4^+ is the more abundant form of deposited N, but it forms only about 10 percent of the total deposited N in urban southern California, depending on the proximity to agricultural sources (Fenn and others 2003; Padgett and others 1999). Some of the fixed N is deposited as wetfall, but up to 90 percent may be deposited as particulate or ionic forms to plant and soil surfaces in the dry Mediterranean summers. The dryfall N accumulates on surfaces until the following rainy season when it is leached into the soil and taken up by plants. Levels of N deposition are high in southern California, with 30 kg per ha per year of N in shrublands (Bytnerowicz and others 1987) and up to 50 kg per ha per year in higher elevation pine forest (Fenn and others 2003). Only the Netherlands has higher levels, up to 90 kg per ha per year, mainly in the form of NH_3 per NH_4^+. These high levels have been experimentally shown to cause loss of shrub cover in heathlands, with a concomitant increase in perennial native grasses (Bobbink and Willems 1987).

Soils in southern California CSS have up to 87 kg per ha per year extractable N measured near urban areas with the greatest atmospheric NO_3^- concentrations (Padgett and others 1999). These high levels of N may also be the cause of the recent exotic grass invasion (Allen and others 1998,

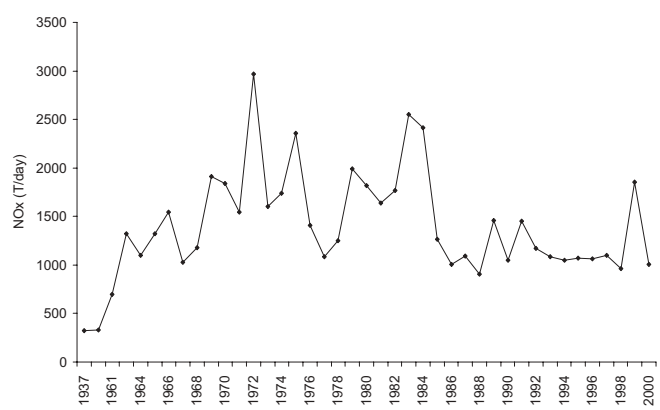

Figure 2—Emissions of NOx in the South Coast Air Basin of southern California, 1937 to 2000 (Alexis and others 2000).

2000). Like cheatgrass in the Great Basin, the Mediterranean brome grasses were introduced to California more than 100 years ago, and some species arrived in the mid-1700s with the first Spanish missions (Heady 1977). Species such as wild oats were abundant in the Central Valley by the mid-1800s where extensive farming and grazing was already underway. But the CSS was also grazed until the early 1900s, and was burned by ranchers to increase annual grass cover (Burcham 1957). However, it appears to have been resilient to permanent vegetation type conversion until the 1960s (Minnich and Dezzani 1998). The Forest Service Vegetation Type Map survey was done throughout California during the 1930s, including some 100 sites in CSS of western Riverside County. Minnich resurveyed these areas in the early 1990s and found that some had lost up to 90 percent of their shrub cover, especially those near urban areas (Minnich and Dezzani 1998). Local botanists have also noted that the diverse native shrubland, with its colorful understory of spring flowers, has converted to monotypic exotic annual grassland in the past 25 to 30 years (for example, Oscar Clark, retired herbarium curator, and Andrew Sanders, herbarium curator, University of California-Riverside).

The simplest explanation for type conversion under N deposition would be that the exotic grasses are responsive to elevated soil N to a greater extent than the native shrubs, as occurred in the Netherlands (Bobbink and Willems 1987), but the situation is more complex in this semiarid climate. Three invasive species, *Bromus rubens*, *A. fatua*, and *Brassica geniculata*, were all highly responsive to N fertilization, but three native shrub species were also responsive, including California sagebrush (Padgett and Allen 1999). Plant response to N in the greenhouse alone did not explain the observed shifts from shrubland to annual grassland, so field studies were initiated. A long-term fertilization experiment was initiated in CSS 40 km south of Riverside, CA, in an area with low N deposition. The site was burned by a wildfire in fall of 1993, and was fertilized yearly thereafter with 60 kg per ha per year of NH_4NO_3 (Allen and others 1998). Annual grasses responded to N fertilizer with an increase in biomass during the wet years, but there were no long-term changes in shrub cover (fig. 3). If there are direct effects of N on shrubs they may be even longer term than this experiment. For instance, species shifts in shortgrass prairie fertilized with 100 kg N annually for 4 years did not materialize until about 5 years after the cessation of fertilization (Milchunas and Lauenroth 1995), so further observations of these plots will continue. However, elevated grass biomass has another impact, which is to increase the fire cycle, and N fertilization may have more immediate effects than species shifts in this vegetation type by altering the fire cycle, as discussed next.

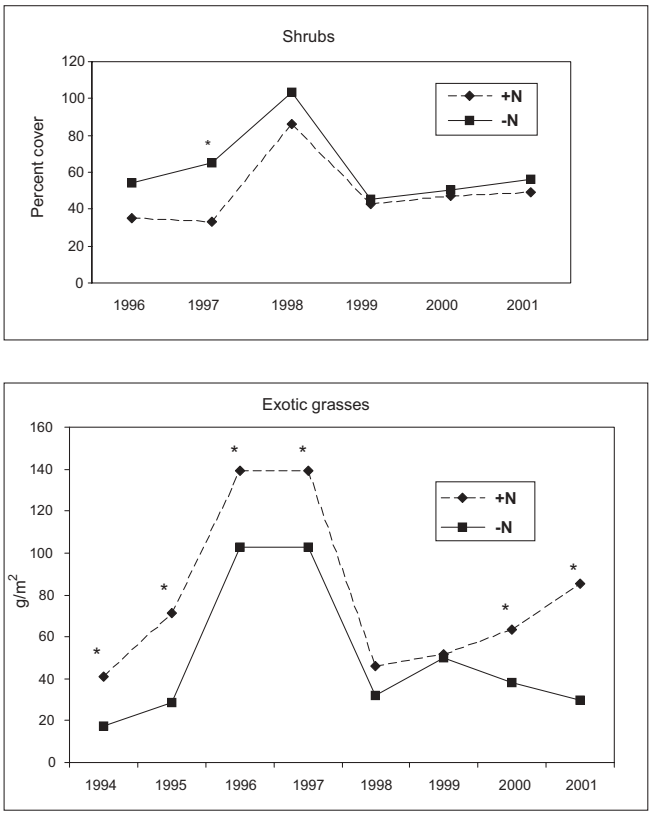

Figure 3—Responses of exotic annual grasses and native shrubs to N fertilization, which was begun in spring 1994 following a November fire in 1993 (data from Allen and others, in press).

Nitrogen and the Fire Cycle

The fire frequency has been reduced from 60- to 100-year to 5-year intervals in big sagebrush-grassland invaded by cheatgrass (Billings 1990; Whisenant 1990). This is largely because cheatgrass forms a fine, continuous fuel that carries fire from shrub to shrub, or from one bunchgrass to the next. Bunchgrasses, like shrubs, are not as efficient at carrying fire long distances (Whisenant 1990). The increase in fine fuel frequency with an increase in the fire cycle has occurred in cheatgrass-invaded lands over the past 100 years, but has only been anecdotally recognized in the past 20 years in CSS. Short fire intervals cause conversion of shrubland to grassland (Calloway and Davis 1993), but short fire intervals can only occur when there is sufficient fuel to carry a fire in subsequent years, for example, following annual grass invasion. The normal fire interval in CSS is about 30 years (Westman and O'Leary 1986). Urban parks in western Riverside County, such as Box Springs Mountain and Mt. Rubidoux, that were dominated by CSS only 20 years ago are now largely annual grasslands because of fires that burn at 2- to 5-year intervals (Cione and others 2002; Minnich 1988). Based on observations from aerial photos, fire frequency probably increased in urban Riverside County in the mid-1960s when persistent patches of annual grasses appeared (Minnich, personal communication). However, even sites that have not burned in 30 years have lost shrub cover, and grass-dominated sites that burned or were disturbed several decades ago have not recovered to their former diversity of native shrubs and understory herbs (Freudenberger and others 1987; Stylinski and Allen 1999). We can learn from cheatgrass-dominated big sagebrush, where initial small incursions of grass promoted fire, which produced a positive feedback loop of grass and fire until an annual grassland stabilized under a frequent fire cycle. Nitrogen deposition will exacerbate the positive feedback by increasing the fine fuel.

Restoration

Restoration is driven by different needs in southern California CSS and in Intermountain sagebrush-grasslands. Fire hazards and large-scale loss of productive grazing lands are primary drivers for restoration in the Intermountain Region, with enhancement of endangered species a secondary or regional issue, depending upon local species occurrence. Conversely, the large number of endangered species coupled with rapid urban development in southern California has created enormous species conservation issues that are in part addressed through mitigation restoration. The fire hazard of CSS located adjacent to urban areas has also increased as fine grass fuels invade, and control of grasses to reduce flammability is a goal in these areas. Rangeland productivity is rarely considered a revegetation goal in CSS any more, because most of the remaining rangelands have been or are being converted to conservation reserves. Where rangeland productivity and fire control of big sagebrush is the goal, revegetation plantings tend to focus on exotic species, while revegetation in CSS nowadays is always done with native plants because of the sensitive species issues. Whether the objective is restoration for rare species or to reduce the fire hazard, the first step is to control annual grasses. A few of the techniques to control the grasses, and their relative success in California and the Intermountain Region, are compared below. These are primarily fire, grazing, herbicides, and mechanical control.

Controlled spring burning of exotic grasses has been used successfully to restore perennial purple needlegrass (*Nassella* [= *Stipa*] *pulchra)* grassland at the Santa Rosa Plateau, a former ranch that is managed by The Nature Conservancy as part of the Riverside County Multispecies Habitat Conservation Plan. While results of fire management from this site are not in the published literature, the managers have demonstrated that late summer or fall burning maintains the annual grass cover, most likely because the seed density is not reduced by fire. By contrast, spring burns before the seeds have shattered enable a complete burn of the potential seedbank. The seedbank of these species is not persistent for many years, with 1 percent or less remaining in the soil after fall germination, so that seedbank control is readily achieved with spring fire (Young and others 1981).

Fire has not been used as a tool to restore weedy CSS because the dynamics of plant response to fire are different in CSS than in grassland. Perennial bunchgrasses resprout immediately after a spring fire, but reseeding shrubs (most species in CSS are reseeders following fire) must compete with residual weed seeds in the seedbank. Prescribed fire has also seldom been used as a tool for restoration of weedy big sagebrush-grassland because native seed banks are often depleted, and cheatgrass will become more abundant with the removal of the shrub cover (Rasmussen 1994). Fire was successfully used to restore native forbs, either seeded or from the seedbank (Wirth and Pyke 2003; Wrobleski and Kauffmann 2003), but these studies were done in areas with low cheatgrass cover. Fires in weedy big sagebrush must typically be seeded because of the lack of a native seedbank (Rasmussen 1994), and similar measures would need to be undertaken in weedy CSS.

Mechanical or herbicide removal of grasses followed by shrub planting is frequently used in CSS restoration mitigation. For instance, grasses (red brome, ripgut brome [*Bromus diandrus*], wild oats) were experimentally thinned by hand to densities varying between 0 and 500 grasses per m^2. Growth of planted California sagebrush was reduced even at the lowest density, 25 grasses per m^2 compared to the control (Eliason and Allen 1997). In another study, control of grasses by mowing or grass-specific herbicide enabled establishment of seeded shrub species, including California sagebrush, but weedy control plots had no shrub establishment at all (Cione and others 2002). Similarly, native plants establish poorly in dense stands of cheatgrass. However, several studies have shown that exotic perennials originating from Asia may readily be seeded into cheatgrass, sometimes even if it has received little treatment to control the annual grasses (Davis and Harper 1990; McArthur and others 1990; Monsen and Turnipseed 1990).

Because of the reluctance to use fire in CSS, studies are underway to control annual grasses and increase shrub and native understory herbs. The study reported here took advantage of the native seedbank, and did not include seeding. The study site is at Lopez Canyon in the Western Riverside County Multispecies Reserve, 55 km south of Riverside, CA, in an area with relatively low N deposition. The area was grazed by cattle until the mid-1980s when it was transferred to Riverside County as mitigation habitat for development of CSS vegetation in other parts of the County. The site was burned by a wildfire in 1993, but has a relatively high proportion of grasses in the understory. The grass invasion may be related to the grazing history of the site. Two treatments, plus an untreated control, were applied in each of three replicate, 1-ha plots: (1) sheep grazing in March per April 1999, 2000, and 2001, and (2) Fusilade (grass-specific) herbicide application in February/March 1999 and 2000. Sheep grazing was done by fencing each of the 1-ha plots, and allowing 200 sheep to remain in each plot for 48 hours. Grazing was done for 3 consecutive years because grasses had already gone to seed the first 2 years, and sheep did not consume the grasses until the third year when more forage was available. Plots were arranged in a randomized block design with the three treatments plus a control in each of the three blocks. Percent cover data of vegetation were collected in 0.5- by 1.0-m plots, 20 plots per ha, in late April/early May of each year. No additional treatments were applied in 2002, but percent cover data were collected.

The exotic grass cover (mainly red brome, with some ripgut brome, wild oats, and annual fescue) decreased with the herbicide treatment in 1999 compared to control plots, and decreased more in 2000 (fig. 4). No additional herbicide was applied in 2001, but exotic grass cover was still significantly lower than in control plots. By 2002 there were no significant differences among the treatments, but this was the driest year on record in this region since recordkeeping began in the State, only about 10 cm in an area that receives 28 cm.

The grazing treatment was not effective in controlling grasses until 2001 (fig. 4). The grazing was done in March, before the data were collected in each year, and showed that the sheep did not consume grasses until 2001. This was the

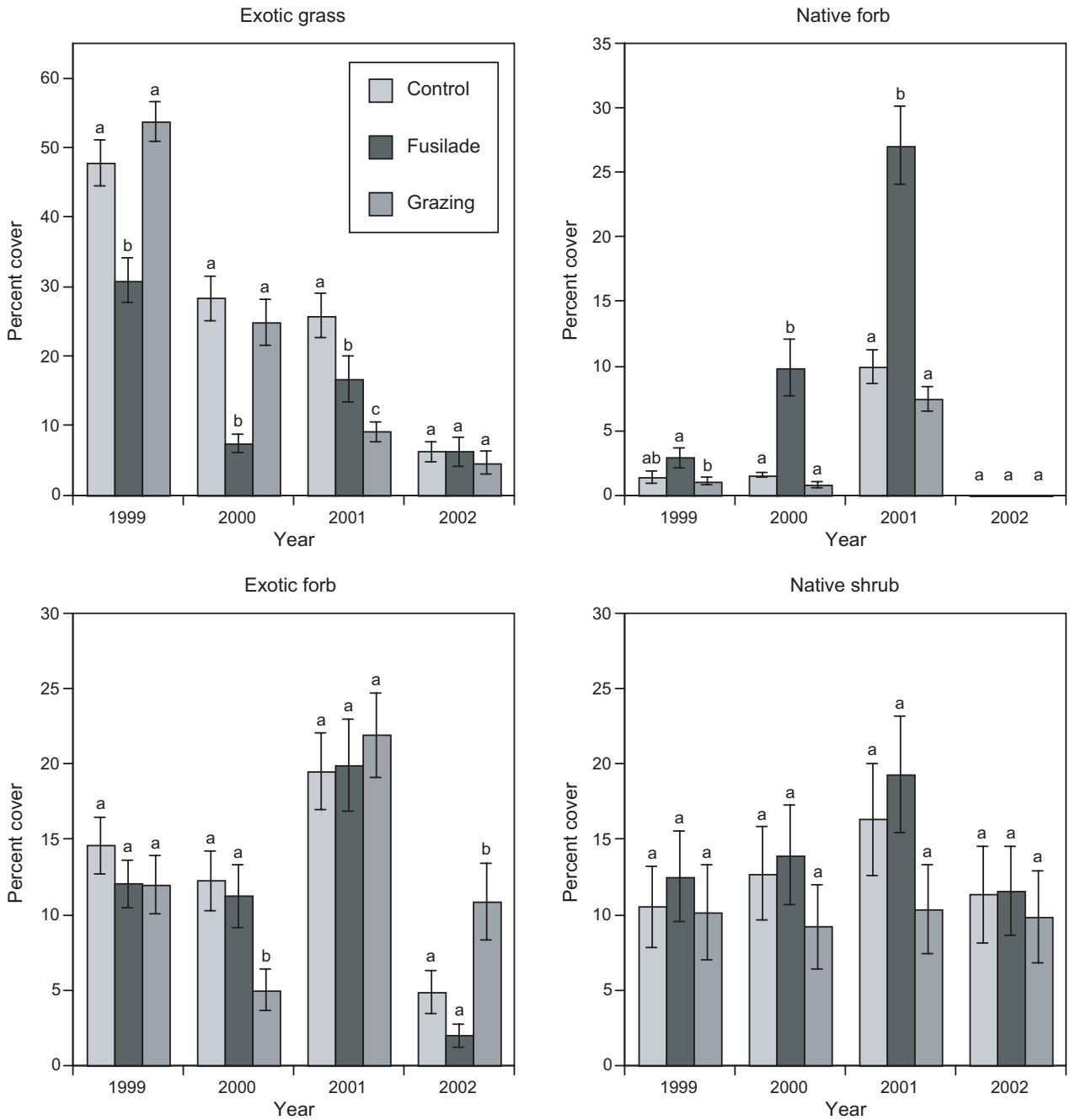

Figure 4—Effects of sheep grazing, grass specific herbicide, and herbicide plus dethatching on percent cover of native forbs, exotic forbs, and shrubs in a coastal sage scrub site in southern California over 4 years. The 2002 growing season was extremely dry, with virtually no germination of native forbs.

only year when the grasses had not produced seed by the time the sheep were placed in the plots. This was not due to poor management, but rather to timing of rains. The rains came late in 1999 and 2000, and by the time grasses had produced forage for sheep to graze, they had also produced seeds. Timing of precipitation was more conducive to annual grass grazing in 2002.

The native forbs consisted of some 20 to 30 annual and perennial species each year, none of which was very abundant individually. Their combined cover increased significantly in the 2000 and 2001 growing seasons in response to the herbicide treatment, but decreased with grazing. In 2002 there was virtually no forb growth at all due to the drought. The sheep consumed the forbs preferentially, but to determine whether the sheep had positive or negative long-term effects on the native forbs the plots will need to be observed for additional years. Whether the native forbs can recover from sheep grazing will depend on the longevity of their

seedbanks. This is likely quite long, as the annuals are largely fire-following species that rest in the soil between the 30-year fire intervals in CSS.

The exotic forbs consisted mainly of storksbill (*Erodium cicutarium* and *E. brachythecium*) with less than 2 percent wild mustard (*Brassica geniculata*), but there were no significant differences among the treatments in any year. Similarly, the native shrubs did not respond in cover to the treatments. We examined the sample quadrats for germinating shrub seedlings, but did not observe any in response to any of the treatments.

Overall, the study showed that native forbs increase in cover following grass-specific herbicide, but there was no improvement of shrub cover. Whether this requires seeding or longer term treatment is unknown. Some of the shrubs have improved germination with smoke or fire (Keeley 1991), so a fire treatment may be needed, but controlled fire is currently unlikely because managers fear further loss of the shrub canopy, as described above.

Restoration at Lopez Canyon will be difficult even without the added grass productivity that comes from elevated soil N. A more difficult case of CSS restoration with high soil N was done in Riverside under high N deposition in a pure stand of exotic grasses. Mowing and herbicide treatments were used to control the grasses so seeded shrubs could establish. There was no native seed in the seedbank, as shown by absence of native plant emergence in weeded but unseeded plots (Cione and others 2002). The addition of mulch is a technique that can help reduce soil N and improve grass establishment. A restoration study on a pipeline disturbance with elevated soil N showed that bark mulch was more effective than straw mulch at immobilizing soil N, and bark also promoted growth of larger California sagebrush plants (Zink and Allen 1998). However, mulching will probably not be a large-scale method of restoration because transporting mulch to large areas is not cost effective. Where grass biomass is high because of ambient or elevated soil N levels, grass control methods are likely more cost effective over large areas than mulch for re-establishment of native vegetation. Cheatgrass-invaded lands may in fact become reduced in N over time due to increased N turnover and leaching (Evans and others 2001), although no change in N dynamics was observed in another study (Svejcar and Sheley 2001).

Conclusions: Vegetation Stability and the Limits to Restoration

The stability of restored vegetation on lands invaded by exotic annual grasses is still in question. California sagebrush and big sagebrush-dominated lands are invasible, at least in part, because the soils are moderate to high in P and N, and subject to N deposition in urbanized California. Annual brome grasses tend to be highly responsive to nutrients, and thus preadapted to these high soil nutrient levels. If the natural vegetation is ecologically unstable and subject to grass invasion, restored vegetation will likely also be unstable. In contrast, some of the most stable revegetated lands once dominated by cheatgrass are those planted to exotic perennials such as forage kochia or crested wheatgrass (*Agropyron cristatum*) in the Intermountain region. Recent hopeful studies show that one native species, squirreltail (*Elymus elymoides*), colonizes cheatgrass naturally, and preferentially allows establishment of sagebrush but not cheatgrass (Booth and others 2003). This may open the door for restoration of big sagebrush, but a similar solution for restoration of CSS is not at hand. Bowler (1990) has stated that the real test of the success of CSS restoration will come after a restored site has burned, and then re-established again. One incident occurred in replanted CSS in Riverside, where a late spring fire burned annual grasses, but adjacent stands of planted shrubs did not burn (Cione and others 2002). The fire did not burn shrubs because of differences in fuel moisture, as grasses were senescent and dry while the deeper rooted shrubs stayed green later into the summer. The goals of a reduced fire cycle and improved forage for grazing can likely be met readily by use of suitable exotic species in cheatgrass-invaded lands, but the more difficult goal of restoration of native plant species and animal habitat will not only require more initial effort, but also long-term maintenance to control invasion of annual grasses.

References

Allen, E. B.; Knight, D. H. 1984. The effects of introduced annuals on secondary succession in sagebrush grassland, Wyoming. The Southwestern Naturalist. 29: 407–421.

Allen, E. B.; Padgett, P. E.; Bytnerowicz, A.; Minnich, R. 1998. Nitrogen deposition effects on coastal sage vegetation of southern California. In: Arbaugh, M., ed. Proceedings of the international symposium on air pollution and climate change effects on forest ecosystems; 1996 February 5–9; Riverside, CA. Gen. Tech. Rep. PSW-GTR-166. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: 131–140. http://www.rfl.psw.fs.fed.us/pubs/psw-gtr-164/fulltext/allen/allen/allen.html#anchor1473574.

Allen, E. B.; Sirulnik, A. G.; Egerton-Warburton, L.; Kee, S. N.; Bytnerowicz, A.; Padgett, P. E.; Temple, P. J.; Fenn, M. E.; Poth, M. A.; Meixner, T. [In press]. Air pollution and vegetation change in southern California shrublands. In: Kus, B. E.; Beyers, J. L., eds. Planning for biodiversity in southern California: bringing research and management together: proceedings of the symposium; 2000 February 29–March 3; Pomona, CA. Riverside, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station.

Bashkin, M.; Stohlgren, T. J.; Otsuki, Y.; Lee, M.; Evangelista, P.; Belnap, J. 2003. Soil characteristics and plant exotic species invasions in the Grand Staircase-Escalante National Monument, Utah, USA. Applied Soil Ecology. 22: 67–77.

Bobbink, R.; Willems, J. H. 1987. Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands: a threat to a species-rich ecosystem. Biological Conservation. 40: 301–314.

Bowler, P. A. 1990. Coastal sage scrub restoration. I. The challenge of mitigation. Restoration and Management Notes. 8: 78–82.

Burcham, L. T. 1957. California range land: an historico-ecological study of the range resource of California. Sacramento, CA: Division of Forestry, Department of Natural Resources.

Bytnerowicz, A.; Miller, P. R.; Olszyk, D. M.; Dawson, P. J.; Fox, C. A. 1987. Gaseous and particulate air pollution in the San Gabriel Mountains of southern California. Atmospheric Environment. 21: 1805–1814.

Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. In: Woodwell, G. M., ed. The earth in transition: patterns and processes of biotic impoverishment. New York: Cambridge University Press: 301–322.

Blondel, J.; Aronson, J. 1999. Biology and wildlife of the Mediterranean region. Oxford University Press.

Booth, M. S.; Caldwell M. M.; Stark, J. M. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. Journal of Ecology. 91: 36–48.

Bowler, P. A. 1990. Coastal sage scrub restoration. I. The challenge of mitigation. Restoration and Management Notes. 8: 78–82.

Callaway, R. M.; Davis, F. W. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. Ecology. 74: 1567–1578.

Cannon, J. P.; Allen, E. B.; Allen, M. F.; Dudley, L. M.; Jurinak, J. J. 1995. The effects of oxalates produced by *Salsola tragus* on the phosphorus nutrition of *Stipa pulchra*. Oecologia. 102: 265–272.

Chiariello, N. R. 1989. Phenology of California grasslands. In: Huenneke, L. F.; Mooney, H. A., eds. Grassland structure and function: California annual grassland. Dordrecht: Kluwer Academic Publishers: 47–58.

Cione, N. C.; Padgett, P. E.; Allen, E. B. 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire and nitrogen deposition in southern California. Restoration Ecology. 10: 376–384.

D'Antonio, C. M.; Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics. 3: 3–87.

Davis, J. N.; Harper, K. T. 1990. Weedy annuals and establishment of seeded species on a chained juniper-pinion woodland in central Utah. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service. Intermountain Research Station: 71–79.

Eliason, S. A.; Allen, E. B.. 1997. Competition as a mechanism for exotic grass persistence following conversion from native shrubland. Restoration Ecology. 5: 245–255.

Evans, R. D.; Rimer, R.; Sperry, L.; Belnap, J. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. Ecological Applications. 11: 1301–1310.

Fenn, M. E.; Baron, J. S.; Allen, E. B.; Rueth, H. M.; Nydick, K. R.; Geiser, L.; Bowman, W. D.; Sickman, J. O.; Meixner, T.; Johnson, D. W. 2003. Ecological effects of nitrogen deposition in the Western United States. Bioscience.

Fiero, B. 1986. Geology of the Great Basin. Reno: University of Nevada Press.

Freudenberger, D. O.; Fish, B. E.; Keeley, J. E. 1987. Distribution and stability of grasslands in the Los Angeles basin. Bulletin of the Southern California Academy of Sciences. 86**:** 13–26.

Gelbard J. L.; Belnap J. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology. 17: 420–432.

Heady, H. F. 1977. Valley grasslands. In: Barbour, G.; Majors, J., eds. Terrestrial vegetation of California. New York: Wiley & Sons: 491–514.

Huenneke, L. F.; Mooney, H. A., eds. 1989. Grassland structure and function: California annual grassland. Dordrecht: Kluwer Academic Publishers.

Jackson, L. E.; Roy, J. 1989. Comparative ecology of annual grasses: native versus Californian habitats. In: Huenneke, L. F.; Mooney, H. A., eds. Grassland structure and function: California annual grassland. Dordrecht: Kluwer Academic Publishers: 81–92.

Keeley, J. E. 1991. Seed germination and life history syndromes in the California chaparral. The Botanical Review. 57: 81–116.

Lesica, P. 1997. Demography of the endangered plant, *Silene spaldingii* (Caryophyllaceae) in northwest Montana. Madroño. 44: 347–358.

Mack, R. N. 1981. Invasion of *Bromus tectorum* into Western North America: an ecological chronicle. Agro-Ecosystems. 7: 145–165.

McArthur, E. D.; Blauer, A. C.; Stevens, R. 1990. Forage kochia competition with cheatgrass in Central Utah. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station: 56–66.

McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. 1990. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service Intermountain Research Station.

Milchunas, D. G.; Lauenroth, W, K. 1995. Inertia in plant community structure—state changes after cessation of nutrient-enrichment stress. Ecological Applications. 5: 452–458.

Minnich, R. A. 1988. The biogeography of fire in the San Bernardino Mountains of California. University of California Publications, Geography. 28: 36–40.

Minnich, R. A.; Dezzani, R. J. 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. Western Birds. 29: 366–391.

Monsen, S. B.; Kitchen, S. G. 1994. Proceedings—ecology and management of annual rangelands. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Monsen, S. B.; Turnipseed, D.; 1990. Seeding forage kochia onto cheatgrass-infested rangelands. In. McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 66–71.

Munk, L. M.; Hild, A. L.; Whitson, T. D. 2002. Rosette recruitment of a rare endemic forb (*Gaura neomexicana* subsp *coloradensis*) with canopy removal of associated species. Restoration Ecology. 10: 122–128.

Nelson, L. L.; Allen, E. B. 1993. Restoration of *Stipa pulchra* grasslands: effects of mycorrhizae and competition from *Avena barbata*. Restoration Ecology. 1: 40–50.

Norris, R. M.; Webb, R. W. 1976. Geology of California. New York: John Wiley & Sons.

Padgett, P. E.; Allen, E. B. 1999. Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. Plant Ecology. 144: 93–101.

Padgett, P. E.; Allen, E. B.; Bytnerowicz, A.; Minnich, R. A. 1999. Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in Southern California. Atmospheric Environment. 33: 769–781.

Pellant, M. 1994. History and applications of the Intermountain greenstripping program. In: Monsen, S. B.; Kitchen, S. G. Proceedings—ecology and management of annual rangelands. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 63–68.

Pellant, M.; Hall, C. 1994. Distribution of two exotic grasses on Intermountain rangelands: status in 1992. In: Monsen, S. B.; Kitchen, S. G. Proceedings—ecology and management of annual rangelands. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 109–112.

Rabinovitch-Vin, A. 1983. Influence of nutrients on the composition and distribution of plant communities in Mediterranean-type ecosystems of Israel. In: Kruger, F. J.; Mitchell, D. T.; Jarvis, J. U. M., eds. Mediterranean-type ecosystems: the role of nutrients. Berlin: Springer-Verlag: 74–85.

Rasmussen, 1994. Prescribed burning considerations in sagebrush annual grass communities. In: Monsen, S. B.; Kitchen, S. G. 1994. Proceedings—ecology and management of annual rangelands. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 69–74.

Stylinski, C. D.; Allen, E. B. 1999. Lack of native species recovery following severe exotic disturbance in southern California shrublands. Journal of Applied Ecology. 36: 544–554.

Svejcar, T.; Sheley, R. 2001. Nitrogen dynamics in perennial- and annual-dominated arid rangeland. Journal of Arid Environments. 47: 33–46.

Young, J. A.; Evans, R. A.; Raguse, C. A.; Larson, J. R. 1981. Germinable seeds and periodicity of germination in annual grasslands. Hilgarida. 49: 1–37.

Waaland, M. E.; Allen, E. B. 1987. Relationships between VA mycorrhizal fungi and plant cover following surface mining in Wyoming. Journal of Range Management. 40: 271–276.

Westman, W. E.; O'Leary, J. F. 1986. Measures of resilience: the response of coastal sage scrub to fire. Vegetatio. 65: 179–189.

Whisenant, S. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., eds. 1990. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 4–10.

Wirth, T. A.; Pyke, D. A. 2003. Restoring forbs for sage grouse habitat: fire, microsites, and establishment methods. Restoration Ecology. 11: 370-377.

Wrobleski, D. W.; Kauffmann, J. B. 2003. Initial effects of prescribed fire on morphology, abundance, and phenology of forbs in big sagebrush communities in southeastern Oregon. Restoration Ecology. 11: 82–90.

Yoder, C.; Caldwell, M. M. 2002. Effects of perennial neighbors and nitrogen pulses on growth and nitrogen uptake by *Bromus tectorum*. Plant Ecology. 158: 77–84.

Young, J. A.; Evans, R. A.; Rageuse, C. A.; Larson, J. R. 1981. Germinable seeds and periodicity of germination in annual grasslands. Hilgardia. 49: 1–37.

Zink, T. A.; Allen, M. F. 1998. The effects of organic amendment on the restoration of a disturbed coastal sage scrub habitat. Restoration Ecology. 6: 52–58.