Air Pollution and Vegetation Change in Southern California Coastal Sage Scrub: A Comparison with Chaparral and Coniferous Forest[1]

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Abstract

The coastal sage scrub (CSS) vegetation of southern California is rapidly converting to annual grasslands, perhaps in part because of air pollution. By contrast, chaparral and coniferous forest are subject to equally high levels of air pollution, but are relatively stable. A comparative analysis of ozone and nitrogen deposition on plants of CSS, exotic annual grassland, chaparral, and coniferous forest shows these vegetation types have different susceptibilities to each pollutant. Historically high concentrations of ozone in the local mountains weakened pines, contributing to tree mortality. Native shrub seedlings had decreased growth in chambers with current-day levels of 150 ppb ozone. Under natural field conditions the shrubs may escape ozone injury by being physiologically active early in the season, when ozone concentrations are below phytotoxic levels. Summer-active pines are more susceptible to ozone than summer-deciduous CSS shrubs and senescent annual grasses. Nitrogen deposition has different impacts from ozone because N accumulates on leaf and soil surfaces during the summer. Conifers are more susceptible to leaf-deposited nitric acid because they are physiologically active in summer, while chaparral may be less so because of thick cuticles and reduced summertime activity. Deciduous CSS and senescent grasses are less susceptible to direct leaf damage. However, N becomes available for root uptake after the first fall rains. Soil accumulation up to 87 μg/g extractable N has been measured in surface soil of CSS shrubland, levels that have caused mortality in the greenhouse. Grasses may escape the deleterious effects of high soil N levels because of their annual habit. Coniferous forest may have a higher threshold for N damage because of high stand biomass, high N immobilization in soil organic matter, and watershed N runoff. The resistance of chaparral to high N is less well understood, but may be due to higher biomass and slower growth rates than CSS, and also high leachate losses of N.

Keywords: nitrogen deposition, ozone, coastal sage scrub, chaparral, coniferous forest, exotic annual grassland

INTRODUCTION

We are currently witnessing a rapid vegetation type-conversion of the coastal sage scrub (CSS) of southern California to exotic annual grassland, a change that has been occurring over the past three decades (Minnich and Dezzani 1998, Allen and others 1998). Local botanists report that mountainsides, such as the Box Springs Mountains and Mt. Rubidoux, that were covered with CSS only 20-25 years ago are dominated by less diverse stands of Mediterranean annual grasses and forbs. In other areas where shrubs still occur, they have exotic-dominated understories, and the native herbaceous species that used to occur have largely been replaced. This directional change in vegetation composition has been attributed to such

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factors as urbanization, fragmentation and corridors that increased weed movement (Zink and others 1995) and historic domestic grazing that removed native species and facilitated weed seed dispersal (Burcham 1957). Frequent fire is creating a positive feedback of increased dominance of highly flammable annual grasses, compared to CSS shrubs that burned on a 25-30 year fire cycle (Minnich and Dezzani 1998). Air pollution, which has less often been considered a factor in vegetation change in CSS, is the focus of this review. Understanding the impact of air pollution for conservation of CSS is critical because it impinges upon vegetation even in those reserves that have been protected from other impacts. Air pollution is greatest in areas dominated by Riversidean sage scrub (Westman 1981), so this CSS association will be emphasized.

As part of this discussion we compare the type-conversion of CSS to annual grassland, with the comparatively stable vegetation in two other major vegetation types of southern California, chaparral and mixed coniferous forest. CSS harbors some 200 sensitive species and is the least widespread of these three vegetation types (Skinner and Pavlik 1994, Sawyer and Keeler-Wolfe 1995). It is the most impacted not only because of air pollution but also because of its location in the most favorable low-elevation private lands planned for development. By contrast, much chaparral and coniferous forest is protected in public lands. However, all three vegetation types are subject to air pollution, both ozone and nitrogen deposition that originate from automobile emissions. Up to 45 kg N/ha/yr are deposited in San Bernardino mixed coniferous forests (Fenn and others 1998), and 30 kg/ha/yr in chaparral in the San Dimas Experimental Forest (Riggan and others 1985, Bytnerowicz and others 1987). All three vegetation types have been impacted by ozone as well, with historical monthly averages as high as 350 ppb in 1975 (Fig. 1).
However, ozone levels have declined with increasing regulation and pollution control, and summertime peak concentrations above 150 ppb occur infrequently. In this analysis we hypothesize that ozone and N deposition have affected vegetation of southern California historically and currently, but CSS, exotic annual grassland, chaparral, and coniferous forest have different sensitivities to the two forms of air pollutants.

To help elucidate the impacts of N on CSS, we present the preliminary results of a N fertilization experiment in CSS vegetation. Anthropogenically deposited nitrate, the dominant form in Riversidean CSS (Padgett and others 1999) is formed from nitrogen oxides, which co-occur with ozone. The concentrations of ozone and nitrogen oxides increase simultaneously along rural to urban gradients of air pollution. To separate the confounding effects of ozone and N, a fertilization experiment was done in a rural area with relatively clean air, at Lake Skinner in the Western Riverside County Multispecies Reserve. The objective of this experiment was to evaluate the longterm effects of N on CSS plant species composition in a controlled field setting, and we present results from the first eight years of fertilization.

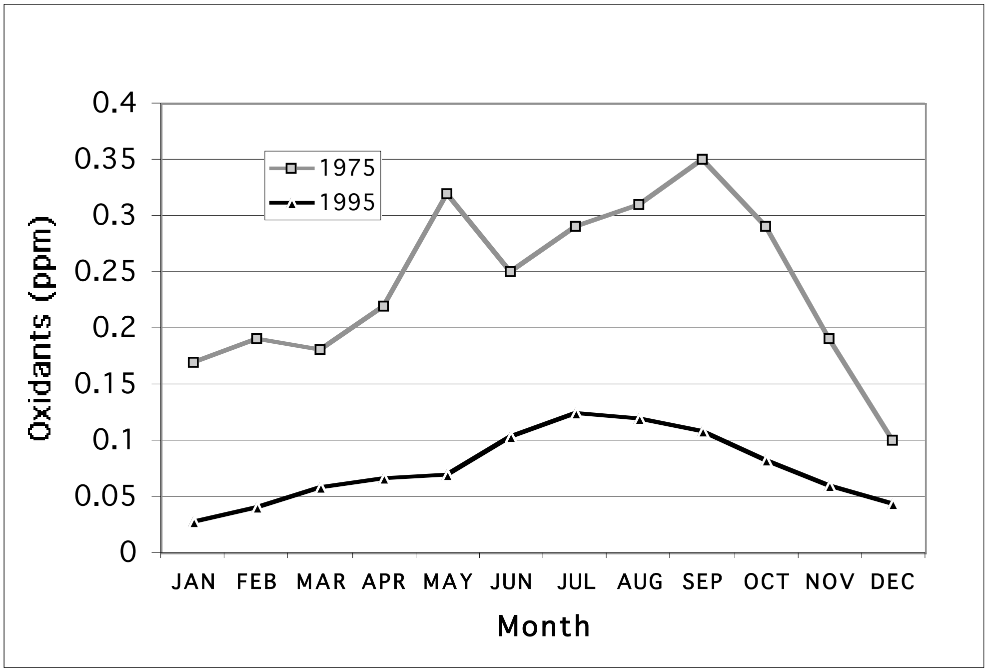


Figure 1—Mean monthly high concentrations of ozone in 1975 and 1995 in Riverside (daily hourly peak values averaged over the month). Different analytical methods were used in 1975 that detected total oxidants, but are corrected to give approximations of ozone (AQMD).

Comparative Air Pollution Effects in CSS, Chaparral, and Coniferous Forest

Ozone

Pinus ponderosa and *Pinus jeffreyi* develop visible ozone damage at daily average levels of 50-60 ppb (Miller and others 1997). The ozone sensitivity of pines was known early from the studies of Miller and others (1963) when levels of ozone were extremely high in the Los Angeles Basin and surrounding mountains. The high concentrations of past decades (Fig. 1) contributed to conifer mortality in the mountains, in part coupled with drought, bark beetle and other stressors (Miller and others 1997). The dead trees from the 1960's and 1970's were often harvested, eliminating the evidence of ozone-induced mortality (Miller 1992, Arbaugh and others 1999). At current reduced levels of ozone, tree mortality does not seem to be a short-term response (Arbaugh and others 1999), but ozone is nevertheless impacting the physiology of trees in the field (Temple and Miller 1994, Grulke and others 1998, Takemoto and others 2000). For instance, at Camp Paivika in the San Bernardino Mountains, ponderosa pine retains 1-2 years of needle growth, rather than the typical five years (Miller and others 1997, Grulke and Balduman 1999). The ground at this site is littered with a deep cover of undecomposed needle litter.

The few available studies of ozone effects on native CSS and chaparral shrubs indicate that visible injury occurs at levels of ozone 2 to 10 times higher than for pines. For instance, seedlings of *Adenostoma fasciculatum, Ceanothus leucodermis, Arctostaphylos glauca,* and *Quercus dumosa* experienced visible damage at the relatively high levels of 100 to 500 ppb ozone (Stolte 1982). Well-watered seedlings of *Salvia mellifera* and *Eriogonum cinerum*, common CSS shrubs, experienced leaf drop and reduced flowering after fumigation in the greenhouse with 100-200 ppb ozone (Westman 1990). One interesting observation that Westman (1990) reported was that the exotic grass *Bromus madritensis* ssp. *rubens* had an ecotype less sensitive to ozone in areas of the Los Angeles basin with high air pollution in the early 1980's.

We have observed mortality of CSS shrubs in the field especially in urban areas (Allen and others 1998, 2000), but the cause of death is not clear and has not been quantified across the landscape. CSS shrubs are summer-deciduous, and are physiologically active mainly in winter and spring (Fig. 2) when mean daily high ozone levels are below 60 ppb (Fig. 1). Thus they may avoid extensive ozone injury by dropping leaves before high ozone exposures occur. Westman (1990) observed that CSS shrubs experienced considerable ozone damage in the Santa Monica Mountains, but his work was done in the mid 1980's when springtime, growing season ozone levels were much higher than today. Maximum hourly summer high ozone levels were 180-390 ppb ozone in the Santa Monica Mountains in 1986 (Westman 1990). Nevertheless, we should not discount the long-term, low level effects of current springtime mean daily high exposures of 50-60 ppb, although short-term chamber studies have shown no acute effects at these levels (Preston 1986).

Chaparral may also be less sensitive to present-day levels of ozone than ponderosa pine and Jeffrey pine. The sclerophyllous leaves of the chaparral dominant *Adenostoma fasciculatum* close their stomates in response to summer drought (Hanes 1965, Poole and Miller 1975) and so are also unlikely to absorb a great deal of ambient ozone in summer at present day levels. By contrast, pines have deep roots that seek water in rock fractures (Hubbert et al. 2001a) and may continue to photosynthesize and absorb ozone all summer long (Coyne and Bingham 1982, Hubbert et al. 2001b). Photosynthesis is lower in summer than spring resulting in lower rates of ozone uptake (Temple 1996), but considerable amounts of ozone may still be absorbed under high summertime ambient concentrations. The phenological differences among these three vegetation types may explain why pine is so sensitive to the high summertime levels of ozone. In 1975 even the springtime ozone levels were as high as 150 ppb (Fig. 1). Had regulations not been enforced to reduce ozone to present day levels, coniferous tree mortality would have continued. The ozone damage symptoms that Westman (1990) observed in CSS shrubs in the mid-1980's would be more widespread, with unknown consequences on mortality. Further reductions in ozone are needed to improve the health of pine forests in locations that currently receive high exposures such as the western San Bernardino Mountains.

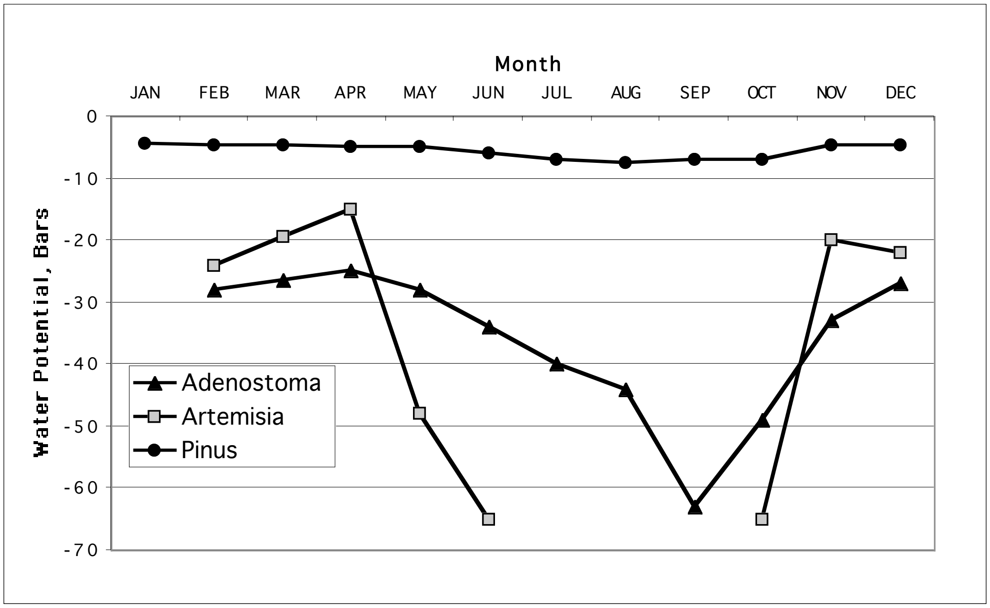


Figure 2—Xylem water potentials of three dominant species of coniferous forest (*Pinus ponderosa*), chaparral (*Adenostoma fasciculatum*) and CSS (*Artemisia californica*). Soil moisture is available during the summer in the coniferous forest where deep rooted trees tap fractured rocks. *Artemisia* and other species of CSS are partially or wholly deciduous in summer, while *Adenostoma* and other chaparral shrubs have small schlerophyllous leaves that close their stomates in response to dry soil. Data from Poole and Miller (1975), Coyne and Bingham (1982).

Nitrogen

Most of the N deposition in southern California occurs as dryfall in the form of HNO_3/NO_3^- originating from automobile exhaust, and about 10-20 percent arrives as NH_3/NH_4^+ from agricultural origins (Fenn and others 1998, Padgett and others 1999) or more depending on proximity to local dairy farms (Fenn and others 2000). The proportion of agricultural input is expected to decline as agriculture moves from the South Coast and Inland Empire counties to the Central Valley and the deserts. While neither form of N input is desirable, NH_3/NH_4^+ acidifies the soil more than HNO_3/NO_3^-, as documented in the Netherlands where up to 90 kg ha^{-1} yr^{-1} of NH_3/NH_4^+ are deposited annually (Bobbink and Willems 1987). CSS soils accumulate up to 87 µg/g of extractable N during summer near Riverside. These soils are not more acid than soils in reserves that have less air pollution, such as Lake Skinner with a maximum of about 20 µg/g extractable soil N in the dry season (Padgett and others 1999). Nitrate has been increasing in soils downwind of urban areas over the past 40 years, with different effects on native and invasive exotic vegetation, as described below.

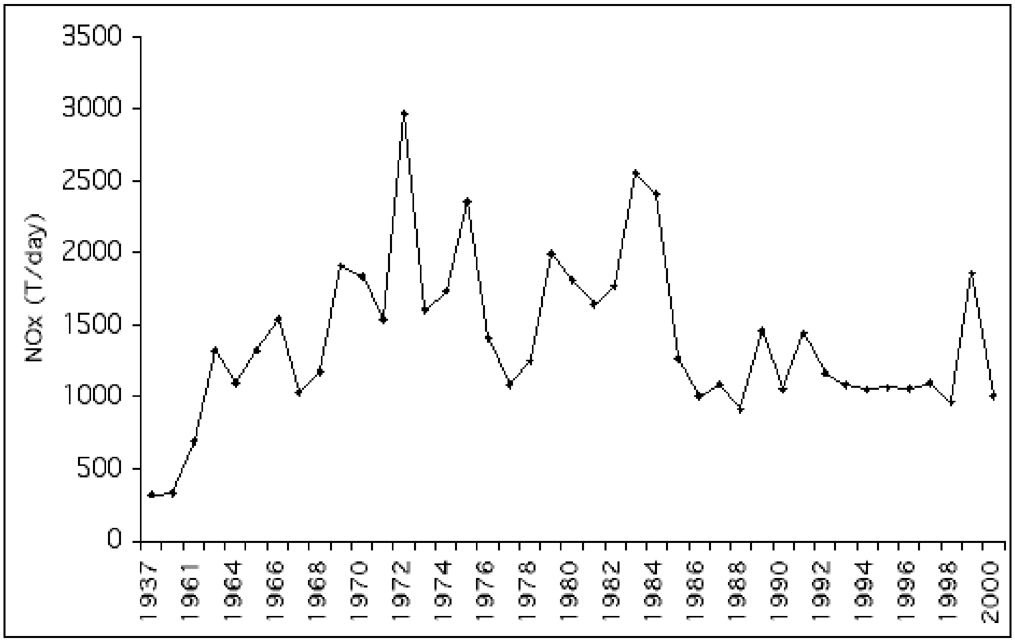


Figure 3—Emissions of NO_X in the South Coast Air Basin, 1937-2000 (Alexis and others 2000).

While historic air concentration data for HNO_3/NO_3^- are not available as for ozone, NO_X emissions have been calculated since 1938 (Fig. 3). These emissions reached a high of nearly 3000 T daily in 1972 in the Los Angeles Basin, and declined to present day levels of 1300 T/dy, except for a rise in 1999 that may be related to La Niña stagnant air conditions. NO_X is converted to NO_3^- in the atmosphere, more so under hot and sunny summer conditions. Most of the N deposition occurs as dryfall during the summer (Padgett and others 1999), although areas with foggy seasons, as occurs in some pine forests in the San Bernardino Mountains, may have high N deposition at that time of year (Fenn and others 2000). Summer-deposited nitrate accumulates on soil and leaf surfaces, and becomes available for plant uptake during the following winter rainy season when it is leached into the soil. Because HNO_3 is sufficiently acidic to cause leaf lesions at high concentrations, dryfall of HNO_3 actually has two separate effects, one to fertilize the soil, and a second to damage the leaf. Some direct uptake of leaf-deposited N occurs also. These different effects of N are considered separately.

Epicuticular leaf lesions, visible using the electron microscope, may be induced by deposition of atmospheric HNO_3 in California blackoak and ponderosa pine (Bytnerowicz and others 1998, 1999). Lesions may be accompanied by structural changes of epicuticular waxes around the stomates. HNO_3 concentrations of 50 ppb for 12 hours were sufficient to cause damage to pine, but oak damage was observed at the higher dosage of 200 ppb. Cuticular damage was observed at ambient levels of 30 ppb HNO_3 in pine and oak under longer exposures (Parry 2001), although long term impacts on plant growth still need to be evaluated. The latter study showed the importance of transcuticular uptake of HNO_3, indicating that even physiologically inactive plants with closed stomates may be subject to damage from HNO3 deposition. CSS shrubs drop most of their leaves in summer, and may be largely unaffected by leaf-deposited HNO_3/NO_3^-. Chaparral shrubs may be protected from extensive nitric acid damage because most of these species have sclerophyllous leaves with thick cuticles, but this is a hypothesis to be tested.

While HNO_3 may cause damage to the leaf surface, it also acts as a fertilizer. As much as one-half of the leaf-deposited N is taken up directly by the stomates into the mesophyll (Bytnerowicz and others 1999). The N that remains on leaf and other plant surfaces may enter the soil via throughfall and stem flow and become available for uptake by roots. In vegetation with a low leaf area such as Riversidean CSS, some of the N will deposit directly on the soil, also increasing the N available to plants. We have done a series of N fertilization experiments to determine whether exotic grasses and forbs have a greater growth response to soil NO_3^- than native CSS plants. In greenhouse and field studies, $^{15}NO_3^-$ was taken up at greater rates by individual *Bromus madritensis* than *Artemisia californica* (Yoshida 1999, Yoshida and Allen 2001). Three exotic species (*Bromus madtritensis, Avena fatua, Brassica geniculata*) had luxury consumption levels of N in their tissues and increased biomass as well (Padgett and Allen 1999). Three native shrub species (*Artemisia californica, Eriogonum fasciculatum, Encelia farinosa*) had continued growth response with increased soil N up to 80 μg/g, but without luxury uptake, i.e. with constant levels of tissue N. These experiments were based on comparisons of individual shrubs with individual weeds, but in the field the weeds are prolific seeders and individual shrub seeds or seedlings are overwhelmed by competition from many individual weedy plants (Eliason and Allen 1997). Additional long-term experiments showed that *Artemisia* and *Encelia* suffer mortality if soil extractable N is maintained at 30-50 μg/g for 6 or more months (Allen and others 1998 and Padgett, unpubl. data). These concentrations probably only occur in surface soils during the dry season in the field, so we do not know whether shrubs may be dying from high levels of N in N-polluted sites in the field. However, exposure to high levels of fertilizer may shorten the lifespan of native plants, as has been shown in botanic gardens (Keator 1994). The annual grasses escape long-term nutrient stress by having a short lifespan with high seed production.

Ongoing N fertilizer studies in the San Bernardino Mountains show that ponderosa pine is responding to N additions of 50 kg/ha with increased diameter growth even in sites that currently receive high N deposition of 45 kg/ha/yr (Fenn and Poth 2001). Levels of excess N are so high that NO_3^- in streamwater is the highest in North America from wildland watersheds (Fenn and Poth 1999). Even so, the available soil N is apparently still limiting during the spring and summer when plants are physiologically active. N fertilization of chaparral caused a small increase in branch length of *Adenostoma fasciculatum* and *Ceanothus greggii,* indicating N deficiency (McMaster and others 1982). This research was performed at the Sky Oaks Field Station, east of Mt. Palomar, in an area that is relatively free of air pollution even today.

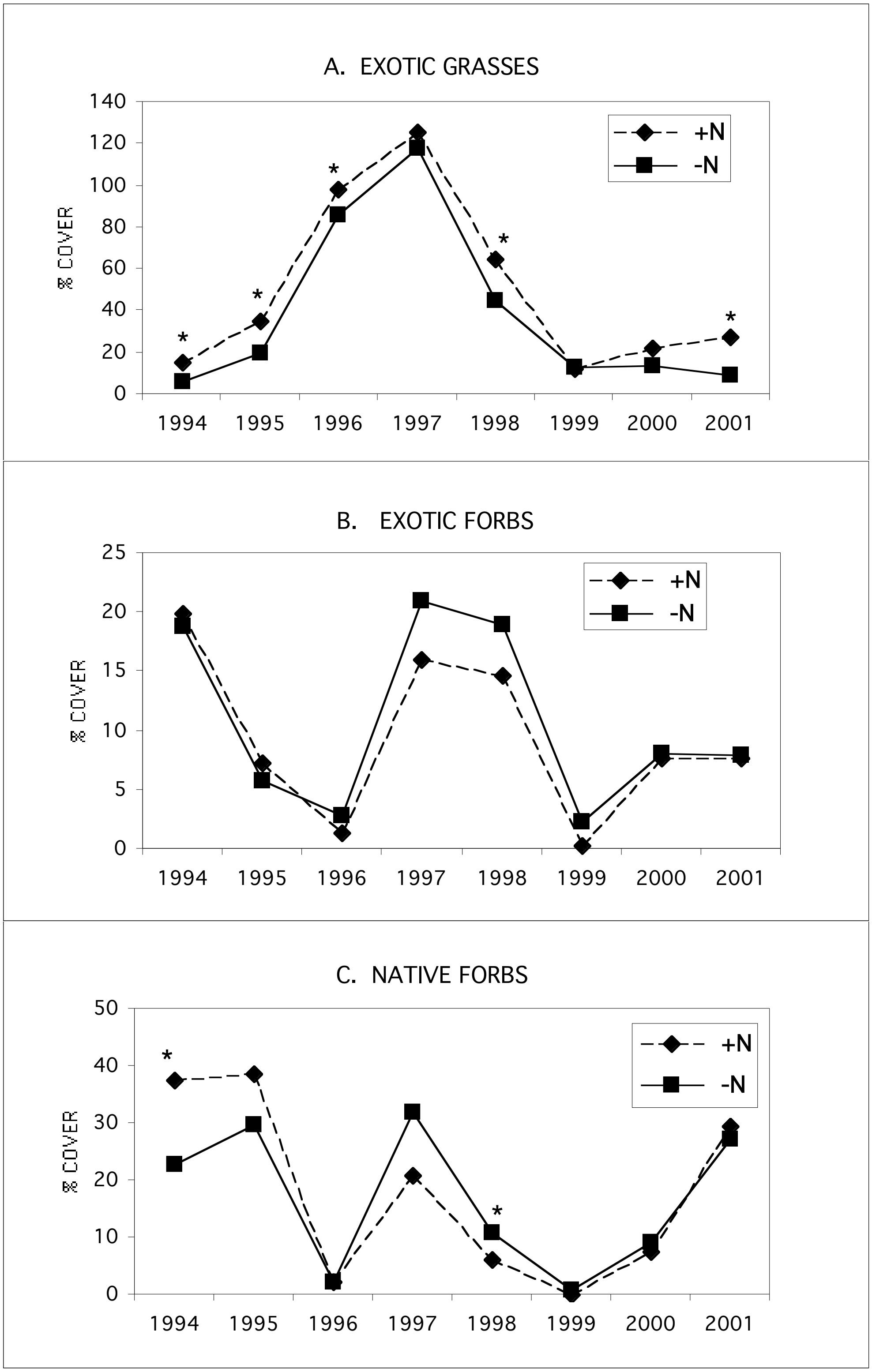
Plants of chaparral have lower CO_2 uptake and lower growth rates than CSS shrubs (Mooney 1988, Hanes 1988) and would not be expected to respond to nutrient additions with rapid growth. In contrast, fertilized CSS shrubs increased their growth and took up N at equivalent or only slightly lower rates than annual weeds, as discussed above (Padgett and Allen 1999, Yoshida and Allen 2001). The loss of shrub cover in CSS is surprising considering the shrubs respond so well to N, so we initiated a field N fertilization experiment to study the interactions of exotic annuals with native shrubs.

Nitrogen Fertilization Experiment in CSS

The effects of N deposition on vegetation can be determined by examining the cumulative effects of long-term changes along a N deposition gradient, and also by conducting N fertilizer experiments in an area that receives low N deposition. Changes in the N gradient along the Riverside-Perris Plain (described in Padgett and others 1999) are confounded by multidimensional changes as for any natural gradient. The co-variance of ozone with nitrogen oxides is the primary concern, but local differences in soil type and fire history also occur, even though sites have been chosen to be as similar as possible. We hypothesized that N deposition or fertilization induces an increase in annual grasses and weeds, and a decrease in shrub cover. The opportunity to begin these studies arose after the November 1993 fires that burned ca. 4000 ha of the Western Riverside Multispecies Reserve. We initiated N fertilizer plots on the north shore of Lake Skinner in the Reserve, where the edge of the fire had burned, and included burned and unburned sites. The unburned CSS vegetation showed very little measurable growth response to N fertilizer, so data from these plots will not be shown here, but the burned site had several notable responses to N fertilization.

Fertilization began in winter/spring 1994 with the application of NH_4NO_3 twice each growing season at 30 kg N/ha for a total of 60 kg $ha^{-1}yr^{-1}$. This rate was chosen to double the highest known deposition in shrublands at the San Dimas Experimental Forest in the San Gabriel Mountains of 30 kg $ha^{-1}yr^{-1}$ (Riggan and others 1985). The fertilizer was applied to 10 plots of 5 X 5 m, which were interspersed in a block design with 10 unfertilized controls. During the first several years when the plots were dominated by herbaceous vegetation, percent cover data were collected in small 0.25 X 0.5 m quadrats. Cover was estimated to the nearest 1 percent by species within a gridded quadrat frame. When shrubs began to get larger, their percent cover was measured using 20 m of line transects within each 5 X 5 m plot, and individual shrub species were counted in the plots to estimate their density. Forb data were collected in April each year when the forbs were at maximum cover, and shrub data in June or July when they had achieved their maximum cover for the year. To calculate grass biomass, a double-sampling technique was used where grasses in additional 0.25 X 0.5 m quadrats were clipped following percent cover estimates. A regression equation was used to calculate the biomass of the unclipped plots.

Exotic grass cover was significantly higher in the fertilized than the unfertilized plots during most years between 1994 and 2001 by 10 to 18


A. EXOTIC GRASSES
% COVER
140
120
100
80
60
40
20
0
1994
1995
1996
1997
1998
1999
2000
2001
+N
-N
*
*
*
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*
B. EXOTIC FORBS
% COVER
25
20
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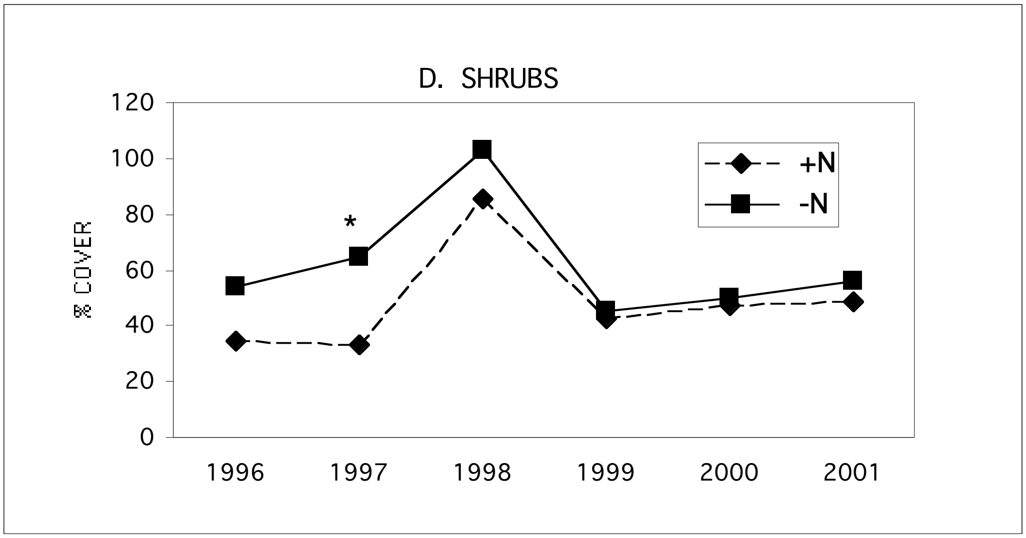

Figure 4—Percent cover of vegetation in plots with and without 60 kg/ha/yr N fertilizer following the 1993 fire at Lake Skinner. Vegetation was analyzed by life form as A. exotic grasses, B. exotic forbs, C. native forbs, and D. native shrubs. * = significantly different at P = 0.05.

percent, becoming similar in the dry spring of 1999 when cover of all species declined greatly (Fig. 4). The species composition of exotic grasses varied somewhat each year, but included *Bromus madritensis, B. diandrus, B. hordeaceous, Avena fatua, Vulpia myuros* and *Schismus barbatus*. For exotic grasses we also harvested biomass, which was considerably higher in fertilized than unfertilized plots during wet years (Fig. 5). The biomass data was a more sensitive indicator of grass response because percent cover did not detect productivity changes that are related to height.

Exotic forb cover was not significantly different in fertilized and unfertilized plots in any year (Fig. 4). The most abundant exotic forbs were *Erodium cicutarium* and *Hypochaeris glabra*. The native forbs responded to N with increased cover during the first year after the fire, but this trend reversed by 1998 (P = 0.06) when they had decreased cover with N. The species of native forbs changed considerably over time, starting with about 26 species of native forbs immediately after the fire and 12 native species by 2001. These are the typical fire-following annuals as reported in other local studies (Carrington and Keeley 1999**).** There was low cover of both native and exotic forbs during the dry springs of 1996 and 1999. The shrubs followed the opposite pattern from the exotic grasses, having significantly lower cover following fertilization in 1996 and 1997, although no longer significantly lower after 1998. Shrub cover also declined during the dry spring of 1999, and did not recover. Shrub cover was very low during the first two years following fire, and was not estimated until the third growing season, 1996 (Fig. 4).

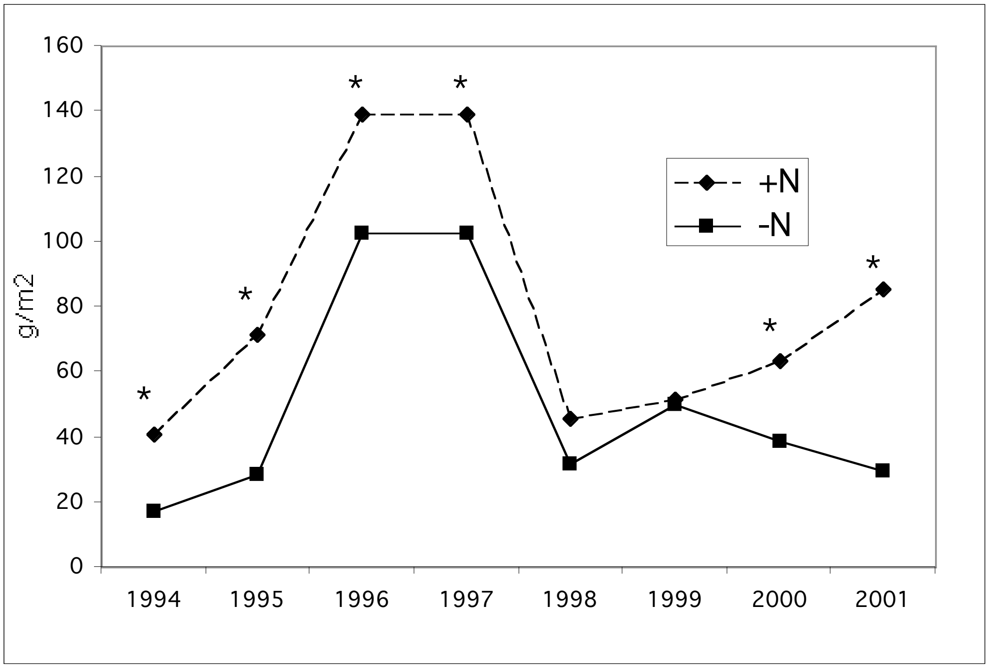

Figure 5—Biomass (g/m^2) of exotic annual grasses calculated from double-sampling a subsample of clipped plots and using a correlation applied to permanent sample plots. * = significantly different at P = 0.05.

The shrubs were dominated by six species (Fig. 6) that each responded differently to N fertilizer. The density of *Malacothamnus fasciculatus* was greatly increased by N fertilization, while that of *Lotus scoparius* was greatly reduced. The only other shrub that responded significantly was *Artemisia californica*, which had increased density with N fertilization. However, *Artemisia* had a relatively low density compared to the two short-lived colonizers *Malacothamnus* and *Lotus*. *Lotus* mortality was highest between 1998 and 1999, accounting for the large drop in shrub cover between those years. Over time the remaining longer-lived shrubs (*Artemisia, Keckiella,* and *Eriogonum*) that dominate mature CSS will fill in, most likely by growing larger in size. Their percent cover was not different between 1999 and 2001, all relatively dry years, but their future rate of growth may be determined by the level of N fertility.

The mechanisms by which N affected growth of the plant species in this stand cannot be determined directly from these field data, but include a combination of individual plant responses to N and yearly climatic conditions, and competitive interactions among groups of species that respond differentially to N. The reduction in *Lotus* with N is expected, as legumes typically respond to N by cessation of N fixation. This makes them less competitive with fast growing neighbors (e.g., Munoz and Weaver 1999). In another study *Artemisia* showed increased growth with N fertilizer in the field both in monoculture and in mixture with grasses (Allen and others 1998). However, it had greatly reduced growth with grass competition in this study, and the N response was too small to overcome the competitive interaction with grasses. The stand studied at Lake Skinner had a relatively high cover of exotic grasses even without N fertilization (Fig. 4). The nearby unburned stands have a patchy understory of exotic grasses, suggesting that exotics were present before the 1993 fire. The exotics may have been introduced by domestic grazing animals, which are responsible for dispersing seeds of many species (Malo and Suarez 1995**).** These lands had been grazed by cattle up to about 20 years prior to the experiment. CSS shrubland in western Riverside County has been widely invaded by exotic grasses and forbs (Minnich and Dezzani 1998), so a site without exotics probably no longer exits. The most important effect of N deposition is likely to facilitate exotic grass dominance. Drought interacted with N fertilizer in our experiment, so that there was no measurable response to N in dry years with low productivity. In addition, the timing of rain may also give an advantage to native forbs, as occurred in the relatively dry 2001 when most rainfall occurred during February. Because the rainfall dynamics have resulted in patterns of plant growth and interactions with N fertilizer, we plan to continue fertilization and observations of these plots for additional years.

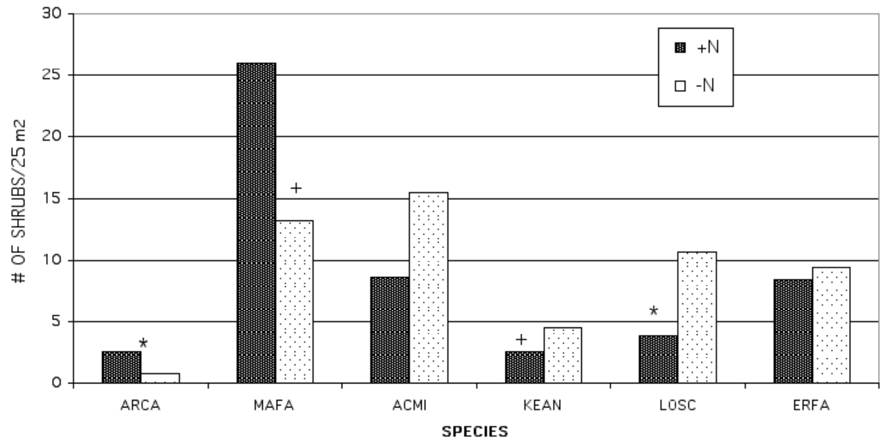

Figure 6—Density of dominant shrubs by species in N fertilized and unfertilized plots. * = significantly different at P = 0.05, + = P <0.10. ARCA = *Artemisia californica*, MAFA = *Malacothamnus fasciculata*, ACMI = *Acourtia microstachys*, KEAN = *Keckiella anthirhinoides*, LOSC = *Lotus scoparius*, ERFA = *Eriogonum fasciculatum*.

Conclusions

The physiological effects of ozone and nitrogen discussed above are summarized in Fig. 7, which shows that CSS, chaparral, coniferous forest, and annual grassland respond differently to the combined effects of these major pollutants. Ponderosa pine forest has negative growth responses to ozone and leaf-deposited nitrate, but the pines still respond to N fertilization of the soil with increased growth. CSS, on the other hand, may be sensitive to elevated soil N as *Artemisia* and *Encelia* experienced mortality in the greenhouse under high soil N (Allen and others 1998). Alternatively, CSS avoids summertime high levels of ozone and leaf-deposited HNO_3/NO_3^- because leaves are deciduous. Chaparral growth response to N has been measured only in a N-limited situation, and it is uncertain how these shrubs respond to high levels of N deposition. It is likely that chaparral would not respond to N fertilizer as well as CSS shrubs, as they are comparatively slow-growing (Mooney 1988, Hanes 1988). Based on these slower growth rates, we would not expect large changes in productivity in N-impacted chaparral, although controlled studies still need to be done. CSS shrubs, on the other hand, continued to grow at high rates with unlimited N, water, and other nutrients, but died after 6-9 months (Padgett and Allen 1999, Allen and others 1998, Yoshida and Allen 2001, Padgett unpubl.).

Vegetation type	O_3	NO_3 soil	NO_3 leaf dep.
Coastal sage scrub	0	⬇	0
Chaparral	0	0?	0
Pine forest	↓	↑	↓
Annual grassland	0	⬆	0

Figure 7—Responses of dominant species of four vegetation types to air pollution stresses. Large and small up and down-oriented arrows represent large or small responses to pollutants; 0 = no or minimal response. Response arrows are based on physiological responses of individual dominant species (see text for references).

The overall “winner” in this race against pollutants is the exotic annual grassland, which is replacing CSS but not chaparral or pine forest. The annual grasses have a high response to N fertilization and they escape ozone and HNO_3/NO_3^- leaf damage by summer dormancy. The summary responses of

Fig. 7 show individual dominant plant growth responses, and do not indicate community or ecosystem level changes and feedbacks that may occur. For instance, during competitive interactions between *Artemisia* and *Bromus*, the grass took up N at greater rates (Yoshida 1999). N deposition also changed the species composition of mycorrhizal fungi in CSS along a nitrogen deposition gradient in the Riverside-Perris Plain (Egerton-Warburton and Allen 2000). Loss of certain mycorrhizal fungal species in high N soils caused a reduced growth response by host plant species, indicating the fungi are no longer effective mutualists (Sigüenza 2000). Many other changes are occurring, such as increases in N mineralization and nitrification rates, and increased litter build-up in N-impacted sites in the mountains (Fenn and others 1996). The forest may be relatively buffered from the effects of elevated N by having a longer lifespan, higher biomass, and soil organic matter to absorb the N. In addition, the mountains experience yearly flushing of accumulated N in snow meltwater and precipitation run-off (Fenn and Poth 1999). There have been some vegetation changes, such as an increase in *Pteridium aquilinum* in the understory at high N sites in the San Bernardino Mountains, but no known changes in the overstory that can be attributed to N.

The reasons for stability of chaparral after N fertilization are not as clear, but may also be related to the open watersheds that experience high levels of N flushing (Fenn and Poth 1999). Chaparral shrubs are long-lived and many resprout from lignotubers following fire. They have slow growth rates compared to CSS, and may not respond to N fertilization with rapid growth. Finally, many stands of chaparral accumulate undecomposed litter except on the steepest slopes, which may enable immobilization of deposited N. Chaparral stands seem to be stable across the landscape (Minnich and Chou 1997), having been affected neither by ozone die-off in the past like pines, nor by possible N impacts as in CSS. However, ecosystems may appear healthy until they reach a threshold of N saturation (Aber 1992). A better understanding of chaparral responses to N is needed before we can be certain that it will remain healthy with continued N accumulation. The dramatic type conversion of CSS to annual grassland should be enough evidence that air pollution levels, especially N deposition, need to be reduced to improve the health of the vegetation.

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