

Nitrogen Deposition Effects on Coastal Sage Vegetation of Southern California¹

Edith B. Allen,² Pamela E. Padgett,² Andrzej Bytnerowicz,³ Richard Minnich⁴

Abstract

*The coastal sage scrub (CSS) vegetation of southern California has been declining in land area and in shrub density over the past 60 years or more, and is being replaced by Mediterranean annual grasses in many areas. Although much of this loss is attributable to agriculture, grazing, urbanization and frequent fire, even protected areas have experienced a loss in native shrub cover. Nitrogen (N) deposition has not previously been examined as a contributor to CSS decline, but up to 45 kg/ha/yr are deposited in the Los Angeles Air Basin. Several mechanisms were examined by which atmospheric N deposition might affect the shrubs and promote growth of weeds. Field nitrogen fertilization studies at sites of high and low deposition showed that most of the abundant native and introduced species had increased growth after fertilization in the low deposition site, but in a high deposition site only one weedy species, small-podded mustard (*Brassica geniculata* (Desf.) J. Ball), responded to N fertilization. Greenhouse studies showed that both shrubs and weeds had high plasticity in their growth response to N fertilizer, an unexpected result for the shrubs. Preliminary competition studies indicated there was no change in the relative competitive ability of the shrubs or grasses after fertilization. However, negative effects of high N have been detected on the growth and survival of the shrubs. Greenhouse grown California sagebrush (*Artemisia californica* Less.) began to senesce at 6 to 9 months when fertilized with 50 µg N/g soil. This soil N concentration corresponds to extractable N levels in polluted sites, while levels are typically less than 10 µg/g in unpolluted sites. Another source of damage to plants can be cuticular lesions caused by nitric acid, but how nitric acid affects CSS leaves is unknown. Fumigation of pine needles with high ambient levels of nitric acid caused cuticular lesions and stomatal collapse, as well as modifications to nitrogen assimilation pathways. The preliminary evidence suggests that CSS vegetation may decline due to elevated nitrate levels in the soil, and additional studies are needed to test effects of ambient nitric acid on CSS leaves.*

Introduction

The coastal sage scrub (CSS) vegetation of southern California has been declining in land area and in shrub density over the past 60 years or more, and is being replaced by Mediterranean annual grasses (Davis 1994, Freudenberger and others 1987, Minnich and Dezzani [In press], O'Leary and others 1992, Zink and others 1995). Although much of this loss is attributable to agriculture, grazing, urbanization and frequent fire, even protected areas have experienced a substantial loss in native shrub cover (Minnich and Dezzani [In press]). Nitrogen (N) deposition has not previously been examined as a contributor to CSS decline, but up to 45 kg/ha/yr are deposited in the Los Angeles Air Basin (Bytnerowicz and Fenn 1996). Nitrogenous compounds in polluted air affect even those tracts of land that have been set aside as reserves, which are in many cases surrounded by urbanization in southern California (O'Leary and others 1992). The coastal sage scrub is of particular interest to conservationists because it supports some 200 sensitive plant species and several federally listed animal species (DiSimone 1995, O'Leary 1989). We need to understand how to manage lands that are influenced by urban air pollution, and whether the biotic communities of these lands can be preserved.

Nitrogen deposition is known to cause vegetation type conversions in other countries, notably the Netherlands (Bobbink and Willems 1987), which have up to 85 kg/ha/yr of N deposited, the highest measured in the world. Nitrogen deposition to reserves is a conservation problem in the Netherlands, where heathlands and species-rich pastures are turning into species-poor grasslands (Asman and others 1989, Bobbink and Willems 1987). The high rates of N deposition in southern California have caused increased soil fertility and surface litter decomposition rates in mixed conifer forests (Fenn 1991), but less is known about

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² Natural Resources Extension Specialist and Associate in the Agriculture Experiment Station, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521-0124. E-mail: edith.allen@ucr.edu, ppadgett

³ Forest Ecologist, Pacific Southwest Research Station, USDA Forest Service, 4955 Canyon Crest Ave., Riverside, CA 92507. E-mail: andrzej@deltanet.com

⁴ Associate Professor, Department of Earth Sciences, University of California, Riverside, CA 92521. E-mail: richard.minnich@ucr.edu

vegetation change with elevated N deposition in this region. The coniferous forests of the San Bernardino Mountains exhibit symptoms of N saturation, such as high N:P ratios in leaf tissue, high soil N, high rates of N loss from the ecosystem, and others (Fenn and others [In press]). If the relatively productive forests of the Los Angeles Air Basin are N-saturated, then less productive vegetation such as CSS that is receiving similar levels of deposition would also surely be saturated. Less productive vegetation may become N saturated more rapidly than highly productive vegetation because the ratio of deposited N to plant biomass is greater, as suggested by Aber and others (1989, 1992) concept of anthropogenic nitrogen saturation. In addition, long-lived trees may respond less rapidly than shorter-lived shrubs, so we may expect to see a more rapid response in vegetation change in CSS than in nearby forests.

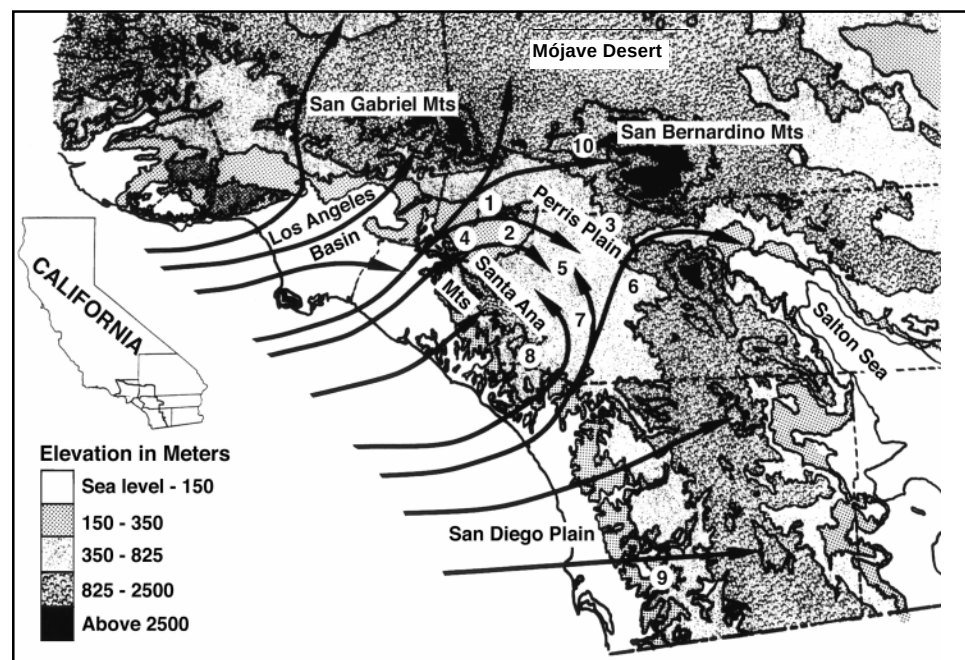
Here we examine the mechanisms by which deposited nitrogen might cause CSS shrubs to be replaced by Mediterranean annual grasses. We present three hypotheses with preliminary data to explain how nitrogen deposition may affect CSS species. Stated in the null form they are 1) CSS shrubs are equally plastic in their growth response to N as are introduced grasses, 2) CSS shrubs are equally competitive as the grasses after N fertilization, and 3) CSS shrub growth and mortality are not affected by high N levels.

Effects of N Deposition on Coastal Sage Scrub Vegetation

We have done series of field and greenhouse experiments on the effects of N deposition on CSS species. The field experiments were done along a gradient of atmospheric N concentrations, using one site with relatively high and another with relatively low N air concentrations for intensive measurements (fig. 1). The high deposition site is at Box Springs Mountain near the University of California, Riverside at an elevation of 670 m, and the low deposition site is some 60 km to the south at the Lake Skinner Reserve, elevation 540 m. Longterm climate data are not available at either site, but the city of Riverside, adjacent to Box Springs Mountain, receives 280 mm precipitation annually. We are still working out the actual deposition rates, which are likely lower than the estimated high values of 30 kg N/ha and more recently 45 kg N/ha at Camp Paivika on the western end of the

Figure 1 — Sample sites on the Perris Plain referenced in the text. The site of highest measured N deposition is Camp Paivika (10) and the site with lowest air concentrations is (9) at Mission Trails Park in San Diego. Arrows show air flow patterns, with polluted air flowing inland from Los Angeles and cleaner air flowing inland from other coastal sites. A convergence zone of polluted and clean air occurs in the middle of the Perris Plain.

- 1 = Jurupa Hills,
- 2 = Mockingbird Reservoir,
- 3 = Box Springs Mountain,
- 4 = Lake Matthews,
- 5 = Motte Rimrock Reserve,
- 6 = Simpson Park in Hemet,
- 7 = Lake Skinner,
- 8 = Santa Margarita Ecological Reserve,
- 9 = Mission Trails Park in San Diego,
- 10 = Camp Paivika, San Bernardino Mountains.



San Bernardino Mountains (Bytnerowicz and Fenn 1996, Fenn and Bytnerowicz 1993). Peak air concentrations were measured with an annular denuder system in August, 1994 as $31.0 \mu\text{g}/\text{m}^3 \text{NO}_3^-$ plus $8.6 \mu\text{g}/\text{m}^3 \text{NH}_4^+$ at Box Springs Mt., and $13.9 \mu\text{g}/\text{m}^3 \text{NO}_3^-$ and $3.9 \mu\text{g}/\text{m}^3 \text{NH}_4^+$ at the Lake Skinner Reserve (fig. 2). Sulfur was relatively low across the gradient, as is the case in other western air pollution measurements (Bytnerowicz and others 1987). The vegetation at both sites is CSS, with a higher proportion of introduced grasses on Box Springs Mountain than at Lake Skinner (Minnich and Dezzani [In press]). Both sites are on granitic soils. Additional sites were used for less intensive measurements.

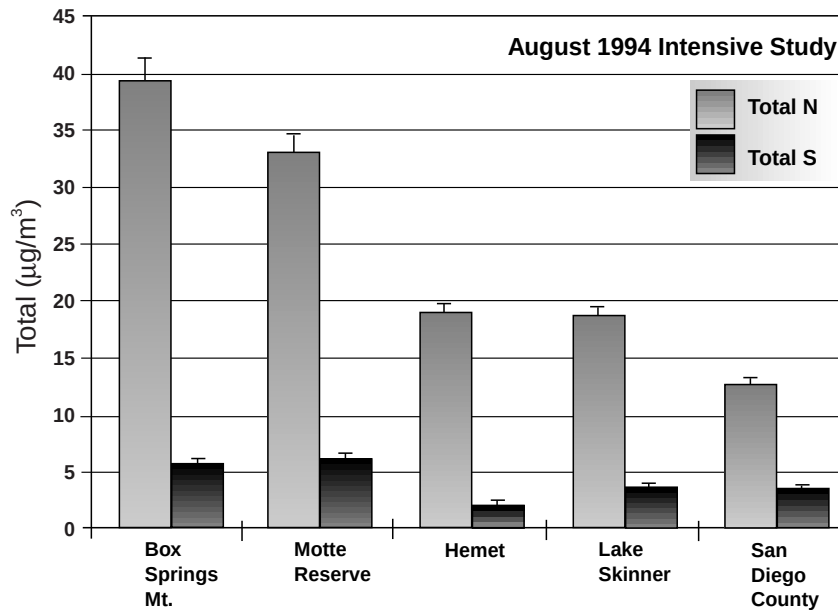


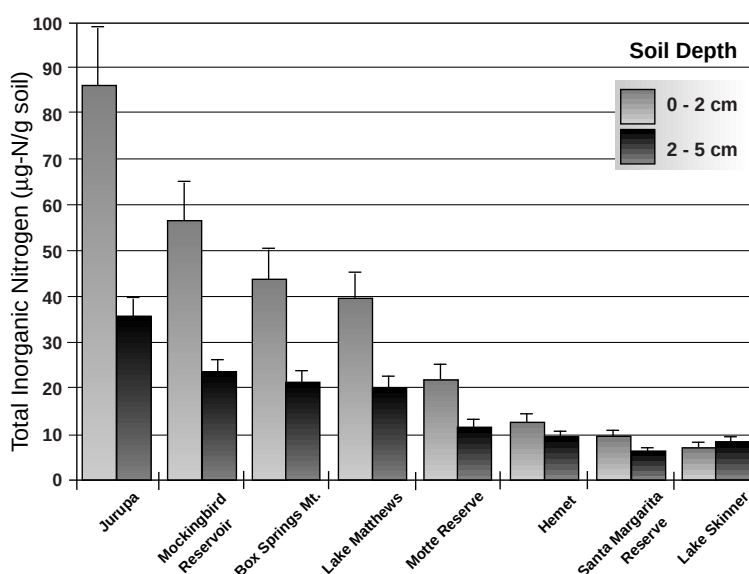
Figure 2 — Nitrogen (NO_3^- -N and NH_4^+ -N) and total S (SO_4^{2-} -S) concentrations in the atmosphere at five sites representing a gradient of air pollution from Box Springs Mountain in Riverside and southward to San Diego during August 1994. Location of sites is shown in figure 1.

In addition to air measurements, soil samples were taken along the gradient of pollution that also included sites to the northwest of Box Springs Mountain (fig. 3). The top 2 cm of soils of the Jurupa Hills had as much as $86 \mu\text{g}/\text{g}$ of extractable N in the form of nitrate plus ammonium (fig. 3), with nitrate predominating at the more polluted sites. Box Springs Mountain had $44 \mu\text{g}/\text{g}$, and Lake Skinner had $8 \mu\text{g}/\text{g}$ of extractable N. These soils were collected in September during the dry season, when soil N accumulates because plants have senesced and are no longer taking up N. The soil N measurements confirm the gradient of N pollution by showing that the soils also accumulate N. We do not yet know if the soil N is higher because of accumulated N deposition, or because of increased mineralization that is induced by N deposition (Fenn and Dunn 1989). However, such high concentrations of N in the soil are likely to affect the plant community, which at each of these sites is CSS with an understory of annual grasses. At some sites, such as Box Springs Mountain and the Jurupa Hills, the annual grasses have become dominant with interspersed patches of shrubs. We explore the mechanisms to explain how the vegetation may change from shrubland to grassland after N deposition.

Plasticity Hypothesis

For one species to replace another in a high N soil, it must have a greater response to N, or in other words be more plastic in response to changes in resources (Jennings and Trewavas 1986). To test this hypothesis, we did N fertilization experiments in the field and the greenhouse. In the field, we fertilized plots at the Box Springs Mountain and the Lake Skinner sites. Both sites had burned in November 1993, and the fertilizer treatments included both burned and unburned vegetation. Each site had ten 5 by 5 m^2 plots and N was applied at a rate of $60 \text{ kg N}/\text{ha}$ as NH_4NO_3 in two doses of $30 \text{ kg}/\text{ha}$ each in February and March, 1994. Plant response was

Figure 3 — Extractable soil nitrogen (NO_3^- -N and NH_4^+ -N) from sites on a nitrogen gradient in September 1995. Soil cores were divided into the upper 2 cm and lower 2 to 5 cm. Location of sites is shown in figure 1.



evaluated in May using non-destructive percent cover data. The unburned plots did not respond to fertilizer at either site with one exception described below, so results of fertilization trials are shown only from the burned plots (table 1).

At Box Springs Mountain only one introduced forb, small-podded mustard (*Brassica geniculata* [Desf.] J. Ball), responded significantly to N fertilizer on the burned plots, and this was also the only species that responded on the unburned plots (data not shown, but small-podded mustard increased from 17 to 29 percent after N fertilization on unburned plots). None of the other introduced grasses and none of the native species responded significantly at Box Springs Mountain in the burned plots (table 1). The introduced grasses included species in the genera wild oats (*Avena*), brome (*Bromus*), fescue (*Vulpia*) and split grass (*Schismus*), while the native species included a diverse mixture of some 70 species.⁵ By contrast, at Lake Skinner almost all of the categories of species, both native and introduced, responded to fertilizer, with the exception of the introduced forbs (table 1). Small-podded mustard occurred infrequently at Lake Skinner, with < 5 percent cover. The total percent vegetative cover was greater in fertilized plots at both sites, but was higher overall at Box Springs Mountain. These results suggest that the plants are N deficient at Lake Skinner, and N saturated at Box Springs Mountain, with the exception of small-podded mustard, which continued to grow and take up N after fertilization. Leaf tissue N of small-podded mustard increased from 3.2 percent to 4.2 percent after fertilization. This suggests that small-podded mustard may be one of the “winners” in the high N deposition zones, as it can take advantage of additional N, even when soil N is already high. The results from the Lake Skinner site suggest that both native and introduced species are plastic in their responses to N, whereas our original hypothesis was that only the introduced species would be highly responsive to N, or “nitrophilous.”

The responses in the field may have been influenced by a number of factors, especially competition in a complex community. To understand the responses of native and weedy plants under more controlled conditions, we performed greenhouse N fertilizer trials of monocultures of three introduced annuals (wild oats [*Avena fatua* L.], red brome [*Bromus rubens* L.], and small-podded mustard), and three native shrubs (California sagebrush (*Artemisia californica* Less.), brittlebush (*Encelia farinosa* Gray.) and California buckwheat (*Eriogonum fasciculatum* Benth.). The plants were grown in 3.5l pots in native soil amended with 0, 10, 50 and 100 µg/g of N as NH_4NO_3 . The soil was collected from the Motte Reserve after scraping off the top 5 cm of soil. After 4 month's growth in the greenhouse, the native shrubs were just as plastic in their responses to N as were the introduced

⁵ Unpublished data on file, Department of Botany and Plant Sciences, University of California, Riverside.

annuals (figs. 4 and 5). In fact, the annuals tended to saturate at 50 $\mu\text{g/g}$, while the shrubs had continued increased growth to 100 $\mu\text{g/g}$. This was an unexpected result, as native wildland species are typically thought to have low responses to nutrient additions compared to weeds and crop plants (Chapin 1980). Clearly the native shrubs are adapted to rapid growth during the brief 4 to 6 month rainy period, at which time they likely take up nutrients as rapidly as possible. The growth period is brief in Mediterranean climates, which have a moist winter and spring but the other seasons are dry. However, in an unpolluted situation, the loading of available N in the soil would not be as great as after N deposition. Our field observations showed that available N built up as high as 86 $\mu\text{g/g}$ in the upper 2 cm of soil (fig. 3) during the dry season, an amount that would be available to newly growing seedlings at the beginning of the next rainy season. Both the native shrubs and the introduced grasses are apparently able to take advantage of this high soil N.

These results were unexpected and not only confound our notions of how plants behave in the wild (the paradigm states they should have slow rates of nutrient uptake and growth), the results also do not explain why N deposition would shift the vegetation from a shrub-dominated to a grass-dominated type. An alternative hypothesis is that competition for N occurs between the grasses and shrubs that is skewed in favor of the grasses.

Table 1 — Percent cover of vegetation in nitrogen fertilized and unfertilized treatments in burned plots at the high N (Box Springs) and low N (Lake Skinner) deposition sites.

Species	BOX SPRINGS			LAKE SKINNER		
	N Fert.	No N		N Fert.	No N	
<i>Brassica geniculata</i>	17.1	9.0	(¹)	0.0	0.0	n.s.
<i>Bromus rubens</i>	15.6	13.5	n.s. ²	4.5	2.0	P = 0.07
Other exotic grasses	20.1	14.7	n.s.	10.5	4.2	(¹)
Other exotic forbs	27.5	26.3	n.s.	19.8	18.9	n.s.
Native forbs	20.7	19.2	n.s.	37.5	22.7	(¹)
Native shrubs	0.0	0.1	n.s.	11.1	4.9	(¹)

¹ Significantly different using a t-test at $P < 0.05$.

² n.s.=not significantly different.

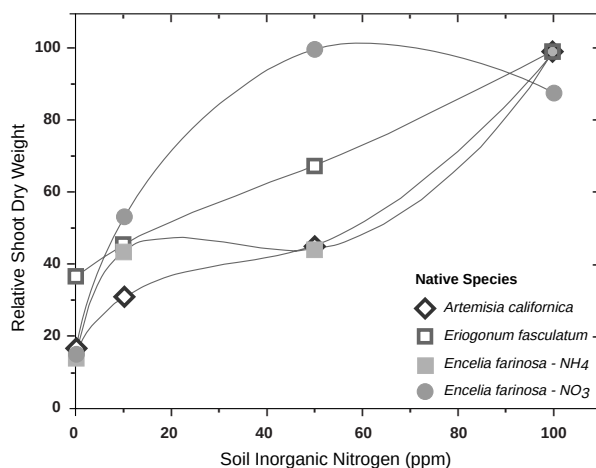


Figure 4 — Relative shoot dry weight of three native shrub species subjected to levels of 0, 10, 50, and 100 $\mu\text{g/g}$ N as NH_4NO_3 in the soil after 4 months of growth. In the case of brittle-bush (*Encelia farinosa*), N was added either as NH_4Cl or as $\text{Ca}(\text{NO}_3)_2$.

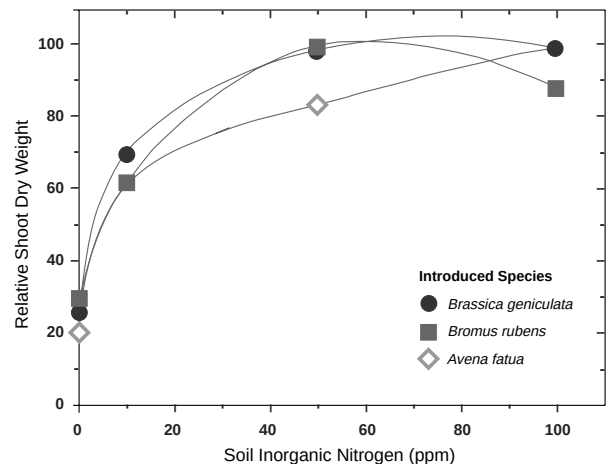


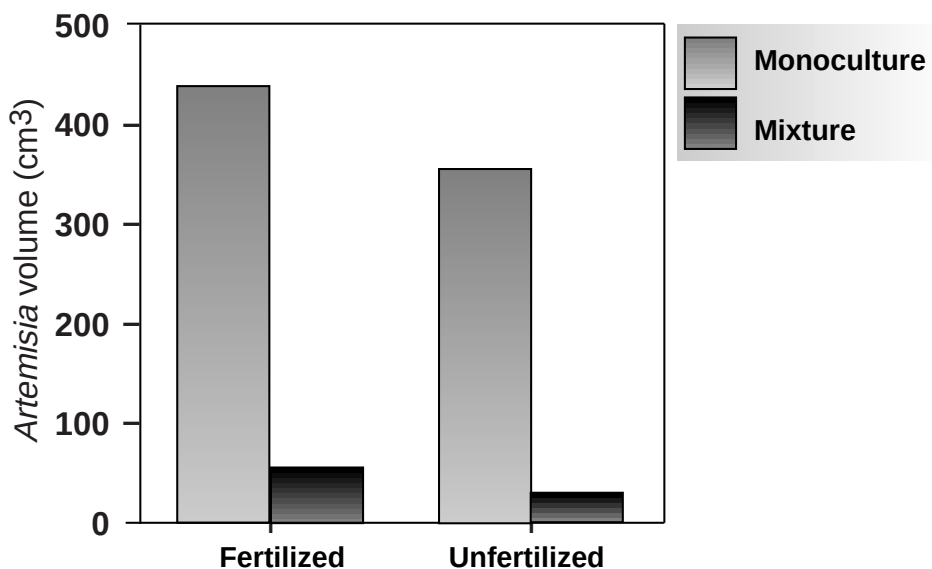
Figure 5 — Relative shoot dry weight of three introduced weed species subjected to levels of 0, 10, 50, and 100 $\mu\text{g/g}$ N as NH_4NO_3 in the soil after 4 months of growth.

Competition Hypothesis

To determine whether N shifts the competitive balance between the grasses and shrubs, we initiated a competition experiment in a patch of introduced grassland that was once dominated by CSS species. This research was done at the Motte Rimrock Reserve about 24 km south of Riverside and intermediate in nitrogen deposition to the Box Springs and Lake Skinner sites. In a blocked experimental design we weeded grasses from ten, 1.2 m² plots and left an additional ten plots as controls dominated by the introduced grasses red brome and foxtail fescue (*Vulpia megalura* Rydb.) A few introduced forbs were also present, mainly species of storksbill (*Erodium*), but few native species. One-half of the cleared plots and one-half of the grassy plots were fertilized with two doses of NH₄NO₃ at the rate of 30 kg N/ha each time in spring 1995. Nine seedlings of California sagebrush were planted in each of the plots in a 2 by 2 factorial design to test two levels of N (0 and 60 kg/ha) and two levels of competition (with and without grasses) on the growth of California sagebrush. The seedlings were spaced 30 cm apart, so they did not interfere in aboveground growth during the first growing season. Because we did not wish to harvest seedlings during the first year, we did non-destructive measurements of height and width to calculate shrub volume. Volume was calculated by assuming that the shape of California sagebrush is spheroid.

The grass competition proved overwhelming for California sagebrush, which had only about one-ninth the volume in the grass plots compared to the cleared plots, with or without N fertilizer (fig. 6). Nitrogen did not shift the balance of competition in favor or against California sagebrush, it only increased the growth of California sagebrush with and without grass competition. Increased growth of California sagebrush after fertilization should be a benefit, if this means that it can survive competition from the grasses. But in fact most of the California sagebrush seedlings in grass plots died during the normal summer drought that followed these measurements, while many survived in the cleared plots. With or without N the seedlings that experienced grass competition were still tiny, and apparently not large enough, or with roots too shallow, to survive the summer drought. On the basis of this experiment, we cannot expect that areas with N deposition will have greater shrub seedling survival. In fact, we noted mortality of mature shrubs in areas of high N deposition, and proceeded to examine potential negative effects of N on shrub growth.

Figure 6 — Volume measurements of California sagebrush (*Artemisia californica*) in weeded (monoculture) and grassy (mixture) plots in the field after 3 months of growth, fertilized with 60 kg/ha N as NH₄NO₃ or unfertilized.



Negative Plant Response to Nitrogen Hypothesis

Because the plasticity and competition hypotheses did not explain why N might cause CSS decline, we continued to test alternative hypotheses. Shrubs in pollution-impacted urban areas have been dying, as can be seen by a walk through Box Springs Mountain County Park and other local reserves. Some 10 percent of the shrubs in the polluted areas that we marked for experimental purposes died during two growing seasons, but we did not experience shrub loss at the Lake Skinner site. We do not yet have an estimate of the rate of mortality on a larger scale, but Minnich and Dezzani [In press] have shown up to a 90 percent loss in shrub cover since the 1930's in urban areas of the Perris Plain (Riverside, California and southward). Shrub loss is lower in the more rural southern Perris Plain. They did their analyses from historic plots in CSS collected by the USDA Forest Service in the 1930's, which they resampled in 1993. Although they showed an increasing pattern of shrub loss toward the urban areas, some factors confounded the results, such as changes in soil type and CSS stand age since the most recent fire at the time of sampling.

Wellburn (1990) explained that N deposition may more frequently harm than fertilize plants, especially in the form of N oxides. We did a series of experiments to determine if elevated N levels might have negative effects on the shrubs. One was a greenhouse fertilization experiment with California sagebrush, where the seedlings were fertilized with 50 μg N/g as NH_4NO_3 . Seeds were planted in a soil of low N, and after they were 3 to 4 months old they were fertilized with the 50 μg N/g soil. They were then fertilized every 2 months to maintain high soil N. During the first 6 months the seedlings grew rapidly, as was noted above. Senescence of individual branches at 6 months, and then complete mortality of all seven replicate plants between 6 and 9 months occurred. At 9 months, and even at 1 year, all of the plants that received low N fertilizer levels were still healthy. These negative effects are difficult to explain, as they appear to be a toxic effect. The soil N we maintained in the greenhouse was not as high as the highest levels we measured in the field, up to 86 μg /g in soils of polluted sites during the dry season. The greenhouse experiment was designed to maintain a concentration of 50 μg /g in the soil during the experiment, with two to three fertilizer additions during the 6 to 9 months. In the field, such a high level would build during the dry season and be maintained only until the beginning of the next rainy season. When vegetation begins to grow again in response to rain, the plants take up the available soil N, and our measurements showed that extractable soil N dropped to 10 μg /g even in the most polluted sites.⁶ Leaching and denitrification might also remove some of the deposited N from the soil, although both of these are probably minor components of the N cycle in this semiarid shrubland. Such high levels of soil N were not maintained throughout the year, so high soil N would not cause as high a rate of shrub mortality in the field as in the greenhouse. But these results do suggest that, over time, high soil N may be a cause of shrub mortality.

The mechanisms by which shrub mortality occurred under high soil N is not known. Horticulturists have long known that native species from soils of low fertility will have short lifespans in a fertile garden, and advise that low fertilizer levels be used for native California shrubs (Keator 1994). We can discuss a number of alternative explanations for the adverse response of native shrubs to high N. It is likely that California sagebrush was taking up large quantities of N, because it has evolved only to take up this limiting nutrient in the soils, not to exclude it. The metabolic requirements for maintaining and detoxifying N in the tissues (NH_4^+ is toxic in high concentrations) may be expensive, and may lead to a shortened lifespan. Assimilation of NH_4^+ requires that carbon be shunted away from sugar synthesis into amino acid synthesis. This would leave a plant deficient in carbohydrates and consequently energy

⁶ Unpublished data on file, Department of Botany and Plant Sciences, University of California, Riverside.

to carry out other biochemical functions. We plan to pursue research on this question, and currently are testing other species of CSS shrubs to determine if this direct effect is generalizable.

Atmospheric N not only causes increased soil N, it results in exposure of vegetation to elevated levels of gaseous and particulate forms of N that may be deposited on leaf surfaces and interact directly with them (Krywult and others 1996). Fumigation experiments have not yet been carried out on CSS species, but they have been done on ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and black oak (*Quercus kelloggii* Newb.). Fumigation with ambient peak summer levels of nitric acid ($50 \mu\text{g}/\text{m}^3$) caused cuticular lesions and stomatal collapse. These adverse responses by leaf surfaces could result in reduced stomatal control and increased exposure of the leaf to other stresses. In addition, nitric acid fumigation caused induction of nitrate reductase and increases in amino acid levels in leaf tissue (Padgett and others 1995). These negative effects can only be postulated for CSS species until similar research is done. Because up to 90 percent of the leaves of CSS shrubs senesce in the summer, there are fewer opportunities for foliar interaction with airborne N at peak summer pollution levels. The CSS plants would be subject to lower spring airborne nitric acid levels.

Conclusions

The decline of CSS vegetation is caused by a combination of complex factors, beginning with direct destruction of CSS for agriculture and urban construction, possibly including past grazing, and also including increased fire frequency in lands that are adjacent to urban areas. But even when these effects are held constant by examining CSS natural reserves that have not been impacted, these shrublands are still declining. The lack of response of the vegetation at Box Springs Mountain to additional N fertilization suggests that it is already N saturated, one response that is cited by Aber and others (1989) as being an indicator of N saturation. However, two forms of air pollution, ozone and N compounds, are likely both central players in the Los Angeles Air Basin and the Perris Plain. We have not discussed ozone in this paper, although it may also play a role in CSS decline. Ozone is known to increase the mortality of conifers in the local mountain ranges (Bytnerowicz and Grulke 1992, Miller and others 1963). Westman (1990) hypothesized that ozone may also be a cause of CSS decline because it reduced the growth of well-watered seedlings in greenhouse experiments at simulated ambient summer concentrations (Stolte 1982). However, during peak summer air pollution conditions stomates of CSS shrubs are closed and many leaves have senesced. Spring ozone concentrations are relatively low, so ozone effects in the field are likely smaller than greenhouse experiments would suggest. The effects of ozone may not be as serious as previously thought in CSS vegetation. However, until our work began, all of the air pollution effects were attributed to ozone and none to N deposition on this vegetation type.

Our studies showed that the annual grasses that replace CSS vegetation are not more nitrophilous than the shrubs, as they have equal plasticity in response to N. However, one species we have tested to date, California sagebrush, suffers a 100 percent mortality rate in the greenhouse in fertilized soils with available N at levels that are no higher than field soils in polluted sites. We are currently conducting experiments with two additional shrub species, brittle-bush and California buckwheat. We have not seen similar results from studies on ozone that would show such a rapid mortality rate. Most studies on ozone report only decreased growth rates at ambient concentrations, not mortality. In addition, the study on toxic effects of nitric acid vapor on pine and oak leaves suggests that more studies of deposited N on CSS shrubs are

needed. Increased mortality of CSS shrubs in N-polluted areas may be a cause of CSS decline in the Los Angeles Air Basin. CSS may be the first vegetation type in the western United States that exhibits stage 3 symptoms of N saturation, which is defined as toxic effects on the vegetation (Aber and others 1989).

Acknowledgments

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