
Cars, Cows, and Checkerspot Butterflies: Nitrogen Deposition and Management of Nutrient-Poor Grasslands for a Threatened Species

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Abstract: *Nutrient-poor, serpentinitic soils in the San Francisco Bay area sustain a native grassland that supports many rare species, including the Bay checkerspot butterfly (*Euphydryas editha bayensis*). Nitrogen (N) deposition from air pollution threatens biodiversity in these grasslands because N is the primary limiting nutrient for plant growth on serpentinitic soils. I investigated the role of N deposition through surveys of butterfly and plant populations across different grazing regimes, by literature review, and with estimates of N deposition in the region. Several populations of the butterfly in south San Jose crashed following the cessation of cattle grazing. Nearby populations under continued grazing did not suffer similar declines. The immediate cause of the population crashes was rapid invasion by introduced annual grasses that crowded out the larval host plants of the butterfly. Ungrazed serpentinitic grasslands on the San Francisco Peninsula have largely resisted grass invasions for nearly four decades. Several lines of evidence indicate that dry N deposition from smog is responsible for the observed grass invasion. Fertilization experiments have shown that soil N limits grass invasion in serpentinitic soils. Estimated N deposition rates in south San Jose grasslands are 10–15 kg N/ha/year; Peninsula sites have lower deposition, 4–6 kg N/ha/year. Grazing cattle select grasses over forbs, and grazing leads to a net export of N as cattle are removed for slaughter. Although poorly managed cattle grazing can significantly disrupt native ecosystems, in this case moderate, well-managed grazing is essential for maintaining native biodiversity in the face of invasive species and exogenous inputs of N from nearby urban areas.*

Carros, Vacas, y Mariposas: Deposición de Nitrógeno y Manejo de Pastizales Pobres en Nitrógeno para una Especie Amenazada

Resumen: *Suelos serpentiniticos pobres en nutrientes en el área de la Bahía de San Francisco sostienen pastizales diversos que soportan muchas especies raras, incluyendo a la mariposa checkerspot (*Euphydryas editha bayensis*). La deposición de Nitrógeno (N) por contaminación del aire amenaza la biodiversidad en estos pastizales debido a que N es el principal nutriente limitante para el crecimiento de plantas en suelos serpentiniticos. Investigué el papel de la deposición de N mediante muestreos de mariposas y poblaciones de plantas a lo largo de diferentes regimenes de pastoreo, revisiones de literatura y con estimaciones de deposición de N en región. Varias poblaciones de la mariposa en el sur de San José se precipitaron después de cesar el pastoreo por ganado. Poblaciones cercanas bajo continuo pastoreo no sufrieron disminuciones similares. La causa de las disminuciones poblacionales fue la rápida invasión de pastos anuales introducidos que saturaron a las plantas hospedero de las larvas de la mariposa. Los pastizales serpentiniticos sin ramoneo de la península de San Francisco han resistido las invasiones de pastos por casi cuatro décadas. Diversas líneas de evidencias indican que la deposición de N seco del smog es responsable de la invasión de pastos observada. Experimentos de fertilización han demostrado que el N del suelo limita la invasión de pastos en suelos serpentiniticos. Las tasas de deposición de N en pastizales del sur de San José son de 10-15 kg ha⁻¹ año⁻¹;*

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los sitios de la península tienen deposiciones mas bajas ($4\text{--}6\text{ kg ha}^{-1}\text{ año}^{-1}$). El ganado selecciona pastos y el ramoneo conduce a una exportación neta de N pues el ganado es removido al ser sacrificado. Sin embargo, el pastoreo pobremente manejado puede desequilibrar significativamente a ecosistemas nativos. En este caso el buen manejo del pastoreo es elemental para mantener la biodiversidad nativa de cara a invasiones de especies y entradas exógenas de N proveniente de áreas urbanas cercanas.

Introduction

Humans have greatly increased the flux of reactive nitrogen (N) in the biosphere, which is now recognized as a major component of global change (Vitousek et al. 1997). Extensive areas downwind of air pollution sources receive substantial inputs of N from wet and dry deposition. Many terrestrial ecosystems are presently N-limited and respond strongly to incremental additions of N, exhibiting changes in productivity, species composition, and nutrient retention. At global scales, N deposition may be responsible for a substantial part of the "missing carbon sink" (Townsend et al. 1996; Holland et al. 1997). At regional scales, N deposition has been implicated in a large number of ecosystem changes, including forest decline in Central Europe (Schulze 1989), grass invasions of heathlands in northwestern Europe (Aerts & Berendse 1988), and changes in grassland composition in the midwestern United States (Tilman 1988). Nutrient-poor ecosystems are particularly vulnerable to N deposition (Aerts & Berendse 1988; Bobbink & Roelofs 1995; Power et al. 1995).

At regional and local scales, N deposition on nature reserves may change vegetation, threaten the persistence of target species and communities, and greatly complicate reserve management. Nitrogen deposition presents a major conservation challenge because the source of the problem is outside the boundaries of reserves and can be controlled only at the source by expensive, long-term measures. Deposition is especially high near urban areas, where combustion sources (primarily cars, trucks, and industrial and home heating) produce substantial concentrations of nitrogen oxides (NO_x). Setting aside reserves on the fringe of urban areas is often difficult, contentious, and expensive, and loss of diversity in reserves because of exogenous factors such as N deposition needs careful consideration.

Native grasslands are among the most imperiled ecosystems in the temperate zones (Joern & Keeler 1995; Samson & Knopf 1996; Muller et al. 1998). Conversion to agriculture and urbanization has left only small remnants of many formerly extensive grassland ecosystems. Remnants are threatened by further development, isolation, invasion by introduced species, and increasingly by N deposition. Grasslands can be sensitive to added N (Huenneke et al. 1990; Wedin & Tilman 1996). Nitrogen fertilization of grasslands generally results in loss of plant

species diversity when a few N-loving species become dominant (Silvertown 1980; Tilman 1987; Huenneke et al. 1990). Losses of plant diversity can lead to losses of animal diversity, especially of host-restricted herbivores.

Many grassland remnants need intensive management from grazing, fire, and mowing. Grazing is a traditional land use in many regions, and poorly managed overgrazing has been responsible for massive disruption of ecosystems worldwide. Yet properly managed, moderate grazing can be a useful management tool in specific instances, especially for species that require short, open grassland (Aerts & Berendse 1988; ten Harkel & van der Muelan 1995). For example, some of the most imperiled butterfly species in England require sheep or rabbit grazing to maintain suitably short grass swards (Oates 1995). Both fire and grazing have been used in management of prairie fragments in the midwestern United States (Samson & Knopf 1996) and have differential effects on butterflies (Swengel 1998). Management of N deposition in grasslands requires the removal of N-containing biomass from a site by fire, mowing, or grazing (Hobbs et al. 1991). Mowing for hay removal in Europe is a common management practice in "unimproved" grasslands set aside for conservation (Dolek & Geyer 1997).

I documented near extinctions of the threatened Bay checkerspot butterfly (*Euphydryas editha bayensis*) in grasslands following the removal of grazing. The proximate cause was the rapid invasion of nutrient-poor serpentine grasslands by introduced grasses. Several lines of evidence indicate that N deposition by air pollution—primarily from cars and trucks—is an ultimate cause of the grass invasion. The negative consequences of improper grazing management in these sites are great, and the story provides a striking example of the complexities of managing reserves adjacent to urban areas and of the interdisciplinary nature of effective conservation biology.

Methods

Study Organism and System

The Bay checkerspot butterfly is restricted to outcrops of serpentine rock in the San Francisco Bay Area, California. Serpentine weathers to a thin, rocky, nutrient-poor soil with low N, high magnesium, low calcium, local patches of heavy metals, and other unfavorable character-

istics. Introduced annual grasses from the Mediterranean region have invaded the majority of California grasslands on richer soils (Huenneke 1989). Serpentinic soils provide refugia for a diverse native grassland with more than 100 species of forbs and grasses (Murphy & Ehrlich 1989), including dense stands of the host plants (*Plantago erecta*, *Castilleja densiflorus*, and *Castilleja ex-certa*) and nectar sources (*Lasthenia californica*, *Layia platyglossa*, *Allium serratum*, *Muilla maritima*, and *Lomatium* spp.) of the Bay checkerspot butterfly. Several serpentine-endemic plants are listed as endangered or threatened (U.S. Fish and Wildlife Service 1998). Numerous patches of these grasslands have been destroyed by urban development (Murphy & Weiss 1988a), and their protection is a major conservation priority in the San Francisco region (U.S. Fish and Wildlife Service 1998).

The Bay checkerspot butterfly is listed as threatened under the U.S. Endangered Species Act and serves as an "umbrella species" for the serpentinic grassland ecosystem (Murphy & Weiss 1988a; Launer & Murphy 1992). As

of 1998, there was one extant population on the San Francisco Peninsula, at Edgewood County Park (EW; Fig. 1). Many former Peninsula populations are extinct because of urban development, and the small population at Jasper Ridge Biological Preserve (JR) appeared to be extinct as of 1999 (S.B.W., unpublished data). The majority of the habitat surrounds the Coyote Valley in south San Jose and supports a reservoir-satellite metapopulation of the butterfly (Harrison et al. 1988). The major sites I considered were the Silver Creek Hills (SC), Kirby Canyon (KC), and adjacent areas of Coyote Ridge (CR) (Fig. 1).

I estimated densities of postdiapause larvae with the stratified sampling design described by Murphy and Weiss (1988b). During the study period (1991–1998), several areas in the Silver Creek Hills were surveyed, along with sites south along Coyote Ridge (CR) and at Kirby Canyon (KC). For conservation planning purposes, the Silver Creek Hills were divided into subareas (SC1, SC2, and SC3) corresponding to property boundaries. Coyote Ridge was subdivided into four areas (CR1, CR2, CR3, and CRlow).

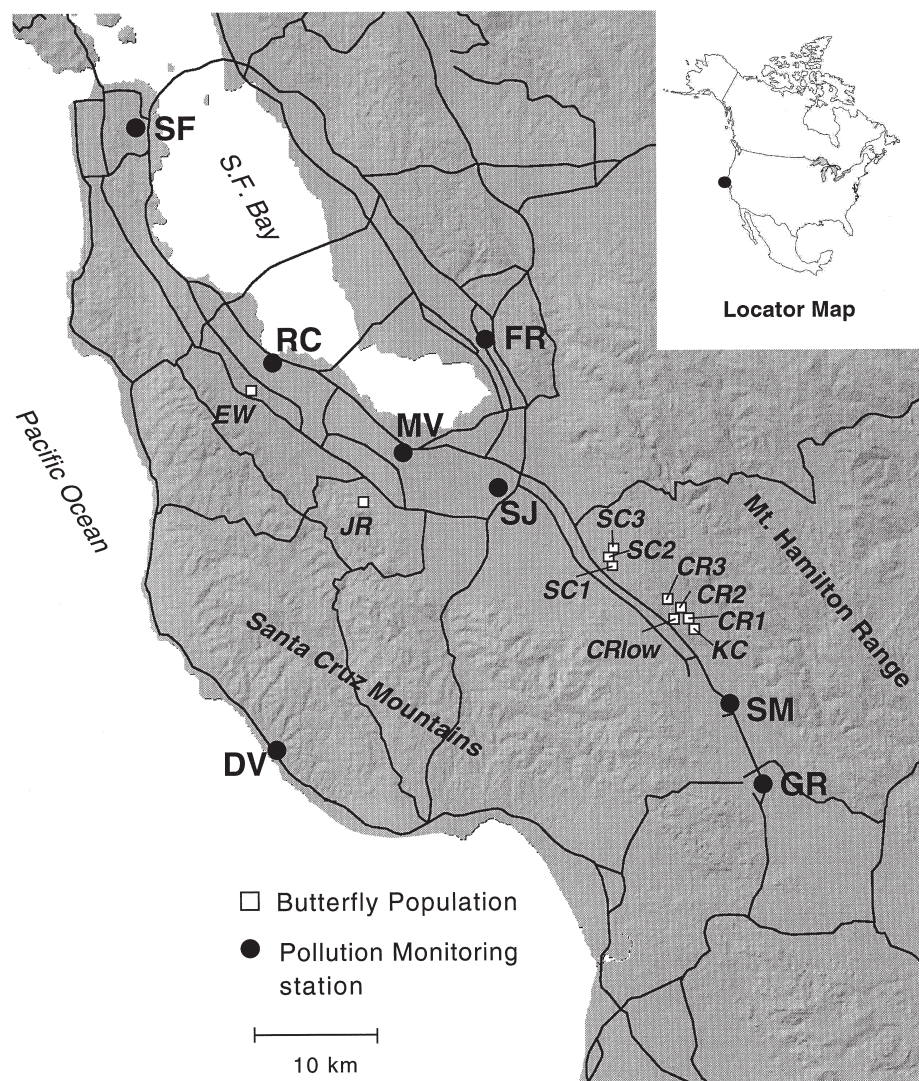


Figure 1. Map of regional air pollution monitoring stations and populations of the Bay checkerspot butterfly in the San Francisco Bay area. Only those air pollution stations and butterfly populations used in this study are identified. Site abbreviations are as follows: KC, Kirby Canyon; CR, Coyote Ridge, numbers 1–3, distinct sites along the ridgetop; CRlow, low-elevation site; SC, Silver Creek Hills, numbers 1–3 are separate properties within the Silver Creek Hills; JR, Jasper Ridge Biological Preserve; EW, Edgewood County Park. Pollution stations are SF, San Francisco; RC, Redwood City; MV, Mountain View; SJ, San Jose; SM, San Martin; GR, Gilroy; and DV, Davenport.

Data on the composition of plant communities across different grazing treatments at KC, CR, and SC were collected in 1996. The treatments were (1) continuously grazed in winter and spring (CR1 and CR2); (2) continuously grazed in summer and fall (CR3); (3) ungrazed since 1990 (SC1); and (4) ungrazed since 1985 (fenced areas adjacent to KC). Transects consisted of five 0.25-m² quadrats spaced 5 m apart and were sampled for percent cover of all vascular plant species. Comparisons of vegetation composition across grazing regimes was limited to undisturbed upland transects that made up the primary habitat for the butterfly. From 1995 through 1998, I sampled three such transects at site SC1 to monitor the effects of reintroduced cattle grazing.

A literature review on the effects of N and other nutrient additions to serpentinitic soils provided data on the response of native and introduced species to fertilization (Turitzen 1982; Koide et al. 1988; Huenneke et al. 1990; Hull & Mooney 1990).

Nitrogen deposition estimates were taken from Blanchard et al. (1996). I modified surface composition and pollutant loads to more closely estimate deposition on serpentinitic grassland in south San Jose. Air pollution data were taken from public documents (California Air Resources Board 1990–1996).

To measure relative deposition among sites, ion exchange resin bags were strung between poles 2 m off the ground at JR, SC, and KC. Resin bag construction and analysis followed standard methods (Reynolds et al.

1997). Twenty bags were hung at each site on 1 October 1997. The poles at Jasper Ridge fell during an intense windstorm on 18 November and were discovered on the ground on 24 November. All JR bags were collected then, and 10 bags each from SC and KC were collected the following day. The JR bags were on the ground for the final 6 out of 54 total days (slightly changing the deposition environment), but the bags were still exposed to reactive N in the air and rainfall. Because those last 6 days also had low pollution levels because of windy, rainy weather, the position of the bags should have made only a minimal difference in the total nitrate collected over the 8 weeks. October–November is the regional smog season, so relative deposition among sites during that period is a good indicator of relative rates over the entire year.

Results

Population Declines of Butterflies

Population estimates in the Silver Creek Hills (SC) showed a pattern of initial growth followed by rapid declines to extinction (Fig. 2). The number of postdiapause larvae rose substantially from 1991 to 1993. From 1993 to 1994, the numbers in the northern section (SC2) fell by a factor of 10. Numbers in the southern section (SC1) fell by 30%. Larval numbers fell from 14,000 in 1993 to 9000 in 1994 in a smaller property (SC3) to the north (not shown on

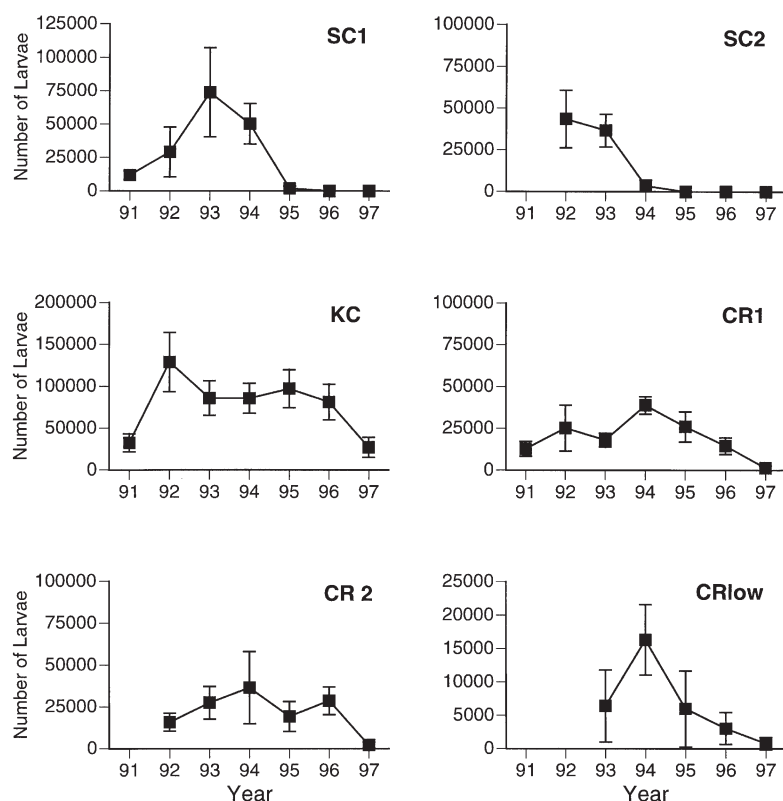


Figure 2. Mean larval densities at sites SC1, SC2, KC, CR1, CR2, and CRlow for the period 1991–1997. Error bars are 95% confidence intervals.

graphs). From 1994 to 1995, larval numbers in SC1 fell by a factor of 20. No larvae have been found at SC1 and SC2 since 1995. Demographic units at KC and CR did not crash over the 1994–1996 time period (Fig. 2).

The cause of population declines was obvious during field surveys (S.B.W. & A. E. Launer, personal observations). Dense stands of *Plantago erecta* and other native forbs were widespread across SC1 and SC2 prior to 1994. By 1995 the grassland was overrun by introduced annual grasses (*Lolium multiflorum*, *Avena fatua*, and *Bromus hordeaceus*) that dominate nearby grasslands on richer soils. *Plantago* was found only on thin soils around rock outcrops and in some areas of gopher disturbance.

The invasion of grasses followed the removal of grazing from sites SC1 and SC2. All three properties in the Silver Creek Hills had been grazed for decades. Grazing was stopped in SC1 in 1989 and in SC2 in 1992, whereas SC3 has been grazed continuously. Although I did not quantitatively sample larval densities in SC3 after 1994 (because of limited access to private property), the grasslands in those areas maintained the forb-rich community typical of serpentine grasslands, and a detectable population of larvae persisted in SC3 through 1997 (R. R. White, personal communication). No larvae were found in either SC1 or SC2, and only three adults were observed in SC1 in 1997. No larvae or adults were observed at SC1, SC2, and SC3 in 1998.

Quantitative Vegetation Data

Qualitative field observations were confirmed by quantitative vegetation data. Vegetation plots from 1996 showed the differences in plant composition between grazed and ungrazed serpentine grasslands in south San Jose (Fig. 3). Both winter-spring and summer-fall grazing regimes had significantly higher densities of *Plantago* and significantly lower densities of introduced

grasses than sites where grazing was removed in 1985 and 1990. The amount of grass cover followed the gradient in grazing intensity and time since grazing removal. Grass cover increased and *Plantago* cover decreased along the gradient from winter-spring grazing (CR1 and CR2), to summer-fall grazing (CR3), to grazing removal in 1990 (SC1), and finally to removal in 1985 (adjacent to KC). Of the introduced grasses that invade serpentine grassland, *Lolium multiflorum* was most common and was responsible for differences among sites (Fig. 4).

At Kirby Canyon in 1985 and 1986, forb-dominated plots within a grazing enclosure that received no fertilization rapidly responded to the removal of grazing (Koide et al. 1988). Following two growing seasons without grazing, grass numbers and biomass greatly increased: by the spring of 1986 *Avena* appeared in forb plots, *Bromus* numbers and biomass tripled, and *Lolium* increased in biomass by two orders of magnitude. *Plantago* maintained high numbers and biomass over the 2 years. By 1987 the enclosure was dominated by dense stands of *Lolium*. *Plantago* and other small forbs were restricted to shallow soils around rocks. Similar plots outside the enclosure retained high forb biomass and low annual grass biomass (Huenneke et al. 1990; S.B.W., personal observation).

Not all serpentine grasslands have been invaded in the absence of grazing. Serpentine grasslands at JR on the San Francisco Peninsula have not been grazed since 1960, have maintained high forb diversity and density (especially *Plantago erecta*), and have not been heavily invaded by *Bromus*, *Lolium*, or *Avena* (Hobbs & Mooney 1995). *Lolium* remained a rare occurrence there until 1998, when it increased greatly during record El Niño rains (S.B.W., personal observation). In contrast, within heavily grazed serpentine grassland at KC and CR during average to dry years, *Lolium* is often found where soils are deeper (Huenneke et al. 1990) and is a substan-

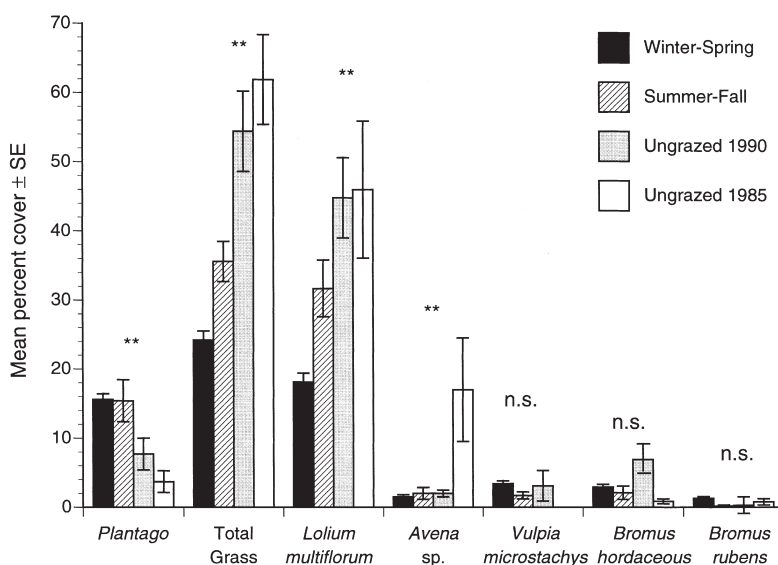


Figure 3. Percent cover of *Plantago* and annual grasses in 1996 at winter-spring grazed, summer-fall grazed, and ungrazed sites (stopped in 1985 near Kirby Canyon, and 1990 in SC1). Grazing was reintroduced at SC1 in 1995. ** $p < 0.001$, Kruskal-Wallis test (nonparametric analysis of variance); n.s., not significant.

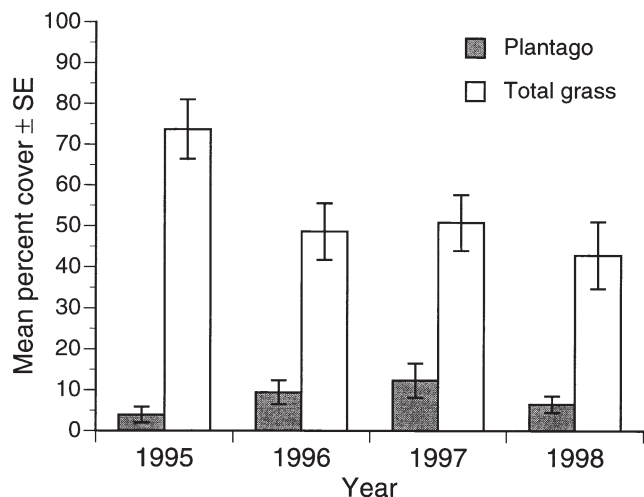


Figure 4. Response of total grass cover and *Plantago* cover to the reintroduction of grazing in site SC1 in summer 1995. Differences in grass cover were significant ($p = 0.01$, Kruskal-Wallis nonparametric analysis of variance), but differences in *Plantago* cover were not.

tial component of the grassland community. Koide et al. (1988) describe "a distinct vegetation patterning present at Kirby Canyon which is not present at Jasper Ridge. This consists of alternating patches of annual forb- and grass-dominated vegetation varying in extent from less than 1 m^2 to greater than 10 m^2 ." In the 1996 vegetation survey, *Lolium* averaged about 20% cover in the winter-spring grazing site (Fig. 3). *Lolium* cover was highest in swales (often $>50\%$) and in deeper soils, but it was also found at low levels (1–20%) throughout the site.

Recovery of Habitat Value

In 1988 the electric fence around the 2-ha enclosure at KC was breached. By 1993, following 5 years of drought, the plot supported high *Plantago* cover, and larval densities (0.25 larvae/m^2) were indistinguishable from surrounding larval samples (S.B.W., unpublished data).

In the summer of 1995 following the population crash, cattle were reintroduced into site SC1. In 1995, grass cover was around 75%, dominated by *Lolium* (Fig. 4). Following 3 years of grazing from 1996 to 1998, grass cover dropped to about 45%. *Plantago* densities did not increase significantly across the habitat, however, but overall forb densities increased from 10% to about 30%, and the habitat appears to be recovering even if the small remnant butterfly population is not (Fig. 2).

Nitrogen Limitation in Serpentinic Grasslands

Experimental work has addressed nutrient limitations in serpentinic grasslands. Nitrogen additions in pots (equivalent of 200 kg/ha) greatly enhanced the growth

of grasses (Turitzen 1982). Fertilization with a nitrogen-phosphorus-potassium slow-release fertilizer (313 kg N/ha/year) stimulated dense growth of grasses at Jasper Ridge (Hobbs et al. 1988). In field experiments at Kirby Canyon, addition of 100 kg N/ha/year into forb-dominated plots stimulated rapid increases of annual grasses (Koide et al. 1988), and factorial design with other nutrients (phosphorus, potassium, calcium) showed that N was the primary limiting factor for grass growth (Huenneke et al. 1990).

Lolium is the introduced grass that accounts for most of the community biomass increases observed under N fertilization (Koide et al. 1988; Huenneke et al. 1990). Detailed studies of *Lolium* and other grasses show that *Lolium* has high N assimilation rates and relative growth rates (Hull & Mooney 1990), and it responds rapidly to fertilization in the field and greenhouse.

Estimates of Nitrogen Deposition

In many regions, such as Europe and eastern North America, wet and dry deposition may be of equal magnitude (Vitousek et al. 1997). Because of the long, dry summer and the winter rains directly off the Pacific Ocean, N deposition in urban coastal California is dominated by dry deposition (Blanchard et al. 1996; Bytnerowicz & Fenn 1996), often by a factor of 10–30. Dry deposition is difficult to measure, and estimates of total deposition rely on models that combine aerial concentrations of reactive-N species with deposition velocities (Hicks et al. 1985, 1987). Deposition velocities are surface specific and may change with meteorological conditions. Expected uncertainties in dry deposition estimates by this inferential method are on the order of 30–50% (Blanchard et al. 1996).

Although the complexities of smog photochemistry and modeling dry deposition fluxes are beyond the scope of this paper, some background is essential (Seinfeld & Pandis 1998). The major N species responsible for dry deposition are (1) nitrogen dioxide (NO_2), (2) nitric acid vapor (HNO_3), (3) ammonia (NH_3), (4) particulate nitrate (pNO_3^-), and (5) particulate ammonium (pNH_4^+). Nitrogen dioxide is formed by oxidation of nitric oxide from combustion in a series of rapid reactions involving ozone (O_3). Nitrogen dioxide is taken up primarily through plant stomata and has a relatively low deposition velocity on inert surfaces. Nitric acid vapor is formed by reactions of NO_2 with hydroxyl radicals ($\text{OH}^\cdot$) on a time scale of hours. Nitric acid vapor "sticks" to virtually all surfaces equally and has a high deposition velocity. Ammonia is produced from soils and animals, and like NO_2 is taken up primarily by plant stomata. Particulate nitrate and ammonium are formed by reactions between soot and dust particles and gases and have relatively uniform deposition velocities among different surfaces.

Blanchard et al. (1996) provide the best current estimates of dry and wet deposition at various sites in California. The only deposition station in the San Francisco Bay area is at Fremont (Fig. 1). Estimated rates of dry N deposition at Fremont were around 6 kg N/ha/year, with 47% from NO_2 and 21% from HNO_3 (Fig. 5a). Wet N deposition at a station in San Jose was 0.89 kg N/ha/year (<15% of dry N deposition) and contributed amounts comparable to NH_3 , pNO_3^- , and pNH_4^+ .

The estimates for Fremont are not directly applicable to the serpentine grasslands from Silver Creek to Kirby Canyon. Several adjustments need to be made for (Fig. 5a): (1) surface composition, (2) seasonality of the grassland, and (3) higher pollution levels. The surface composition used for deposition modeling in Fremont was 70% inert surface (asphalt, roofs, etc.), 15% grass, and 15% tree. When 100% grass was used, deposition from NO_2 increased from 2.2 to 5.2 kg N/ha/year because NO_2 has a much higher deposition velocity on grass than on inert surfaces. Ammonia deposition increased from 0.91 to 2.9

kg N/ha/year. Nitric acid vapor deposition did not change appreciably because it has similar deposition velocities on all surfaces. The total deposition at Fremont for a 100% grass surface was estimated at 10 kg N/ha/year (C. Blanchard, personal communication.).

Nonirrigated grasslands in California are green in the rainy season (November–April) and largely brown in the dry season (May–October). Deposition varies seasonally because proportions of N species vary over the year (Fig. 5b). Nitrogen dioxide deposition is highest in fall, whereas HNO_3 deposition is highest in summer. To simulate this seasonality, the figure for 100% grass was used only for the fall and winter months, whereas the figure for the “urban” mix was used for the spring and summer. At Fremont this adjustment reduced deposition to 100% grassland to 9 kg N/ha/year (Fig. 5a)

South San Jose has more air pollution than Fremont. Deposition from a N species is generally proportional to concentration. The ratio in annual NO_2 concentration between San Jose and Fremont is around 1.3 (Fig. 6a), and the ratio of pNO_3^- concentrations is around 1.2 (Fig. 6b, both comparisons $p < 0.01$, paired t test by year). Increasing ozone levels (Fig. 6c) indicate that HNO_3 increases toward the south because there is generally a tight relationship between ozone and HNO_3 vapor in polluted areas (Blanchard et al. 1996). The ratio of 1:1.2 in ozone concentration between Fremont (FR) and San Martin (SM, the site closest to Kirby Canyon, paired t test by year $p < 0.01$) suggests a 20% increase in HNO_3 deposition. Based on these adjusted pollutant concentrations, the estimate for dry deposition into seasonal grassland in San Jose increased to 11 kg N/ha/year (Fig. 5a).

The average yearly input of wet deposition at San Jose has been 0.89 kg N/ha/year for a total of around 12 kg N/ha/year. Wet deposition within a region usually varies proportionally with rainfall. Because the ridgetop at KC receives about 640 mm rainfall, twice that at the wet deposition station in San Jose (330 mm), wet deposition at Kirby Canyon is estimated to be about 1 kg N/ha/year greater. Given uncertainties in deposition calculations, 10–15 kg N/ha/year is a reasonable approximation for sites such as Silver Creek and Kirby Canyon.

Jasper Ridge lies upwind of most pollution sources and receives much of its air as northwest winds off the Pacific Ocean that pass over the virtually undeveloped Santa Cruz Mountains (Fig. 1). Marine air is low in NO_2 , as evidenced by low levels at Davenport, directly on the coast (Fig. 6c). That prediction is confirmed by the resin-bag sampling. Aerial bags at JR collected about 40% of the NO_3 , compared with bags at SC and KC (JR = $2.3 \pm 1.1 \mu\text{g/mL}$ extracted, SC = $5.3 \pm 1.1 \mu\text{g/mL}$, KC = $6.8 \pm 0.7 \mu\text{g/mL}$, mean $\pm$ SE, $n = 4$ for all sites). The difference between JR and two other sites was highly significant ($p < 0.001$), but the difference between SC and KC was not (Tukey-Kramer HSD test). If that ratio holds for total deposition throughout the year, then JR may receive about 4–6 kg N/ha/year.

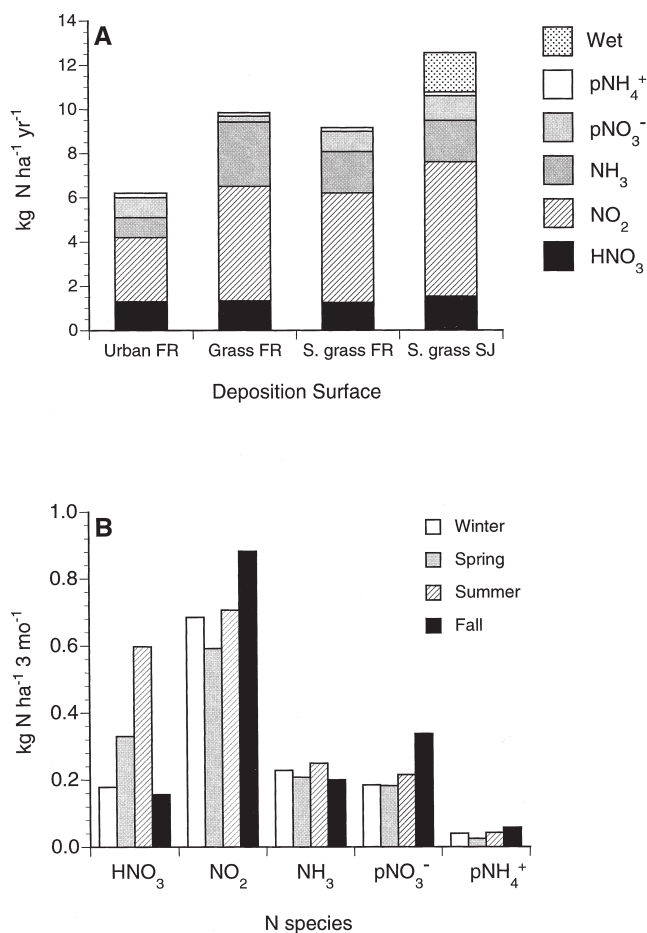


Figure 5. (a) Adjusted estimates of nitrogen deposition for grassland and seasonal (S) grassland at Fremont (FR) and San Jose (SJ). (b) Seasonality of nitrogen deposition by species at Fremont, California. (Adapted from Blanchard et al. 1996.)

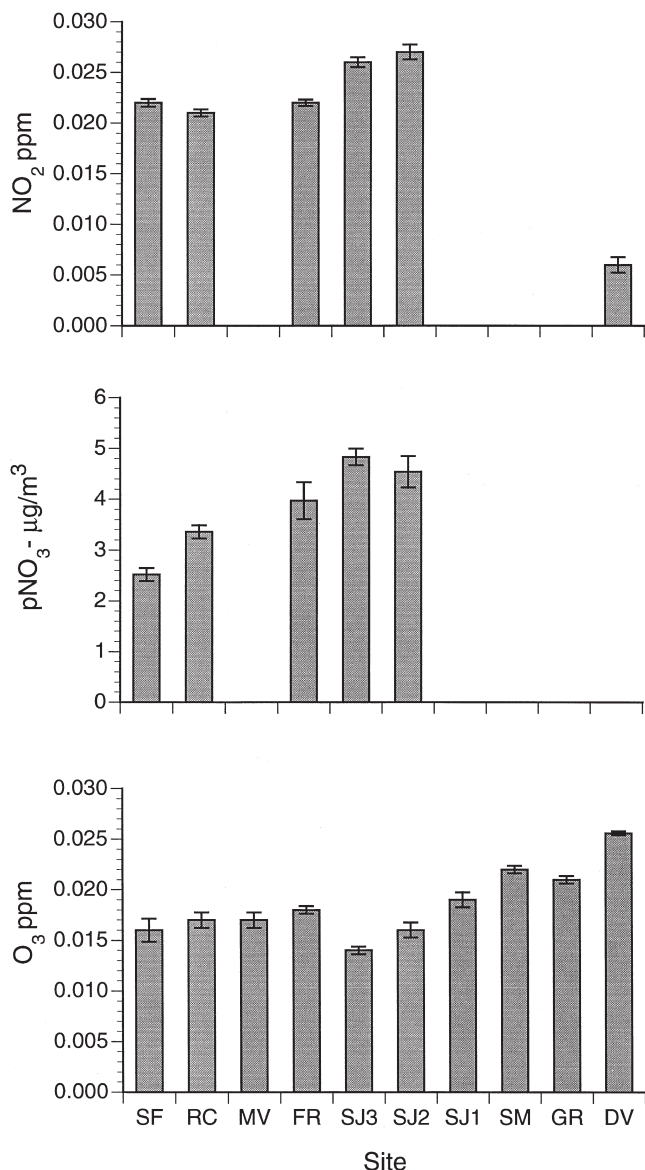


Figure 6. Annual average concentrations (1990–1996) of ozone, NO_2 , and particulate NO_3^- at pollution monitoring stations in the San Francisco Bay area (data from California Air Resources Board 1990–1996).

Discussion

The population surveys showed that the Bay checkerspot butterfly experienced severe population crashes in 1994 and 1995 after grazing was removed from two sites in the Silver Creek Hills. Concurrently, other populations in continuously grazed areas did not crash, indicating that widespread climatic factors such as drought were not responsible for the population crashes at SC1 and SC2.

The proximate cause of the crashes was invasion by introduced grasses. The dense sward of grasses, espe-

cially *Lolium multiflorum*, reached heights of 0.75 m and crowded out small native annual forbs, especially *Plantago erecta*. Similar invasions of serpentinitic soils by annual grasses have been observed around the Santa Clara Valley (Ehrlich & Murphy 1987; Murphy & Weiss 1988a; Huennike et al. 1990). Extensive serpentinite outcrops in Santa Teresa County Park, where grazing was eliminated in the late 1970s, are dominated by grasses (S.B.W. & A. E. Launer, personal observation). Few if any checkerspot butterflies are found in ungrazed areas. Similar grass invasions have not occurred at JR, despite the removal of cattle grazing in 1960.

These observations suggest a fundamental difference between JR and the south San Jose sites. My review of experimental work showed that serpentinitic grasslands are largely N limited and can be rapidly invaded by introduced grasses when N is added. The most responsive species is *Lolium multiflorum*, the most common grass at ungrazed sites in south San Jose. *Lolium* has been rare or absent from Jasper Ridge.

I estimated that N deposition levels in grasslands in south San Jose are 10–15 kg N/ha/year. Total deposition may be even greater. My calculations did not include nitric oxide (NO), which may also dry-deposit into grasslands (Hanson & Lindberg 1991); average NO concentrations are not reported, nor was NO included in the Blanchard et al. (1996) estimates. In addition, areas of bare soil typical of serpentinitic grasslands may have high deposition velocities for NO_2 , greater than that of the plants themselves (Judeikis & Wren 1978; Hanson et al. 1989). Nitrogen deposition levels at Jasper Ridge are much lower, based on local meteorology and preliminary measurement with aerial resin bags.

These levels of N deposition in south San Jose are high enough to act as fertilizer and enhance the growth of annual grasses at the expense of native annual forbs. Over the course of several years, the amounts of N deposition at SC and KC approach the yearly amounts used in fertilization experiments. Most grassland ecosystems respond incrementally to N additions (Tilman 1988). For example, the effects of the addition of 50 kg N/ha/year on annual grass growth were intermediate between 0 and 100 kg N/ha/year in field experiments at JR (Hull & Mooney 1990). Serpentinitic grasslands are highly retentive of N (Reynolds et al. 1997; Hooper & Vitousek 1998), and leaching losses are small (Hooper & Vitousek 1998). Thus, incremental additions of N are incorporated into plants and microbes and may build up over several years.

The magnitude of dry N deposition flux in south San Jose is comparable to the measured yearly N uptake by plants in serpentinitic grasslands. Hungate et al. (1997) measured plant N uptake at 30–50 kg N/ha/year. Hooper (1996, personal communication) estimated similar uptake in high-diversity experimental plots. A substantial portion of dry deposition (especially NO_2) is directly absorbed by stomata and is ready for immediate assimilation into the plants.

The evidence indicates that N deposition is greatly affecting the habitat suitability of serpentine grasslands for the threatened Bay checkerspot butterfly and other native species. Invasion of grasses following grazing removal is not a subtle phenomenon, can occur rapidly, and takes many years to reverse. Given the repeated responses of these grasslands to the removal of cattle grazing, the key conservation recommendation is that well-managed, moderate grazing must be maintained on sites that are expected to support the butterfly. Any conservation plan that sets aside land must include long-term grazing management.

The mechanisms by which grazing directly and indirectly affects the plant community and the N cycle are diverse. Most directly, cattle selectively graze introduced annual grasses in preference to forbs. The taller grasses can rapidly outgrow shorter forbs; grazing maintains a low, open plant canopy. Grasses also outcompete native forbs through buildup of dense thatch (Huenneke et al. 1990). Cattle break down the thatch by trampling and feeding in the dry season. Cattle also disturb the surface and compact soils, but the effects of this disturbance alone on plant composition are not well understood.

Grazing effects on the N cycle are complex. On an ecosystem-wide basis, cattle remove N as they gain weight and are removed for slaughter. Some N may also be exported via ammonia volatilization from droppings and urine (Holland et al. 1992). Although cattle droppings and urine lead to local deposition of N, in terms of N, cattle "eat globally and deposit locally." Local fertility islands (<1 m²) immediately around cattle droppings support lush stands of annual grasses (usually *Lolium*). Cattle grazing can also lead to enhanced N availability in the soil by speeding up the rate of N cycling via allocation patterns of plants (Holland et al. 1992).

Grazing regimes must be well managed and of moderate intensity. The rancher at KC and CR regularly monitors cattle weight gain and grass availability. When biologists asked for removal of cattle from KC during drought years to prevent overgrazing, the rancher had already made the decision to move his cattle to other pastures. This self-regulation of the grazing regime has been a great benefit for the Bay checkerspot butterfly and for many of the native plant species that survive on serpentine soils.

The butterfly also persists in areas where grazing is concentrated in the summer and fall. Although grass cover is higher in these areas than in the winter-spring grazed areas (Fig. 3), *Plantago* and numerous nectar sources are still abundant. Multiple management regimes may help to spread risks associated with particular grazing regimes. For example, grazing during the winter and spring undoubtedly leads to some direct mortality of butterfly larvae, eggs, and pupae by crushing; this source of direct mortality is avoided by summer-fall grazing at the cost of higher grass cover in the habitat.

Some plant species do not do well with grazing. *Dudleya setchellii* (listed as endangered) lives on rock outcrops, is often chewed up by cattle, and tends to be more abundant and vigorous in ungrazed areas (U.S. Fish & Wildlife Service 1998; personal observation). Fencing off selected rock outcrops that provide little habitat value for the butterfly is effective mitigation. Grazing may not be the perfect solution to grass invasions, but, given the current state of our knowledge, existing moderate grazing regimes appear to be a suitable management prescription for most serpentine grasslands in south San Jose.

Ungrazed, grass-dominated sites can recover to acceptable levels of habitat quality for the butterfly following the reintroduction of grazing, but recovery may take years. Introduced grasses perform well during wet years and poorly during droughts, and *Plantago erecta* performs well during droughts (Hobbs & Mooney 1995). The years following reintroduction of grazing in SC1 (1995–1998) all had above-average rainfall, including the record El Niño winter of 1997–1998, so grass growth was favored. Conversely, a severe drought period may slow the grass invasion and speed recovery; recovery of the KC grazing enclosure took place over 5 years of drought.

Fire and mowing may not be appropriate management tools for serpentine grasslands. Fire in these grasslands is poorly studied, and extensive controlled experimental studies would be required to properly assess the effects of fire. Fire may kill Bay checkerspot larvae that are in summer diapause beneath rocks and in the soil. Mowing and hay removal are not feasible because of rock outcrops and steep slopes.

Documenting the effects of grazing removal creates a dilemma for scientists and conservationists attempting to protect biologically rich serpentine grasslands. Removal of grazing is a rapid route to diminished habitat quality and population-level extinctions of the one protected species that can stymie broad development plans on serpentine soils. One landowner (SC2) has already followed that course in hopes of eliminating the habitat value from his parcel. The U.S. Fish and Wildlife Service (1998), however, is aware of the problem and still regards the degraded habitat as important to protect. Whether the Endangered Species Act can be invoked to force landowners to continue grazing is an open question.

Although N deposition on the peninsula is lower than in south San Jose, it still may have chronic long-term effects. *Lolium* may require several years of drier weather to disappear from JR. Edgewood Natural Preserve, which has consistently supported patches of high-density *Lolium* throughout the grassland (S.B.W., personal observation), may be affected by short-range deposition from an eight-lane freeway that bisects the site. Introduction of grazing or fire at EW and JR would be difficult without careful research and planning to address scientific and political concerns.

The ultimate solution is to eliminate sources of excess N, a much larger societal problem that will take decades to solve. Air pollution standards based on direct human health issues may not be stringent enough to avoid negative effects on N-sensitive ecosystems. The San Francisco Bay area (and all of California) presently meet federal and state standards for mean annual NO_2 concentrations (California Air Resources Board 1996). Cars are the major regional source of NO_x (60% or more), and little progress has been made in reducing car use despite chronic traffic problems. Proposed new air quality rules will only incrementally decrease NO_x levels and offer no short-term relief.

The threads of this story highlight the interdisciplinary nature of conservation biology. Much of the evidence linking N deposition to the grass invasions is still circumstantial and inferential. More research is needed in a number of areas: (1) refinement of deposition estimates; (2) effects of low-level chronic N additions over several years; (3) effects of grazing regime on serpentine, both in terms of plant composition and N dynamics; (4) time course of restoration following the reintroduction of grazing; (5) recovery of Bay checkerspot populations; and (6) alternatives to grazing, especially fire. Such research would necessarily draw on atmospheric chemistry, plant ecology, ecosystem ecology, range management, population biology, and other disciplines and would be a major, long-term research program.

The number and identity of rare species in California beyond the Bay checkerspot butterfly that are being negatively affected by N deposition is unknown. Dry N deposition in California varies greatly with location (Blanchard et al. 1996): 24–29 kg N/ha/year in the Los Angeles Basin; 10–20 kg N/ha/year in Central Valley cities (Bakersfield and Sacramento); 6 kg N/ha/year in Fremont and Santa Barbara; and around 1 kg N/ha/year in rural locations at Gasquet (far northern California) and at Sequoia and Yosemite National Parks in the Sierra Nevada. Other estimates of N deposition in California range up to 45 kg N/ha/year in forests in the San Bernardino Mountains in the Los Angeles basin, which are showing signs of N saturation (Bytnerowicz & Fenn 1996). Coastal sage-scrub communities are being transformed by the invasion of annual grasses driven by N deposition (Allen et al. 1998).

Conclusions

The enhancement of the global N cycle is but one aspect of global change. Land-use alterations and invasive species are two widely recognized components of global change (Vitousek 1994), and the plight of the Bay checkerspot butterfly demonstrates how all three factors interact to threaten local biological diversity. Land-use change (urbanization) directly threatens the serpentine grasslands of the San Francisco Bay area (Murphy & Weiss 1988a). The invasive grasses that have dramati-

cally changed California's grasslands are poised to dominate the last refugia for the native grassland flora and fauna, given the chance. That chance is provided by smog-induced fertilization, but only with the additional land-use change of removing grazing. The economics of grazing adjacent to major urban areas may not be viable over the long term. It is ironic that grazing, which has contributed so greatly to the transformation of California's native grasslands, may prove necessary for their maintenance on nutrient-poor soils downwind of major pollution sources.

Nitrogen deposition is a long-term regional and global problem that deserves increased attention from scientists and policymakers (Vitousek et al. 1997). Many other rare ecosystems, communities, and species worldwide may be affected by N deposition from nearby (or even distant) air pollution sources. The effects of additional N may be obvious, as observed in this study, but also may be more subtle, such as changes in soil chemistry and plant tissue that can affect herbivores and overall nutrient cycling. Identification of the problem and establishment of suitable management regimes will undoubtedly take much research and experimentation by conservation biologists and managers.

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