



Review

Nitrogen critical loads and management alternatives for N-impacted ecosystems in California

M.E. Fenn^{a,*}, E.B. Allen^{b,c}, S.B. Weiss^d, S. Jovan^e, L.H. Geiser^f, G.S. Tonnesen^g, R.F. Johnson^{b,c}, L.E. Rao^b, B.S. Gimeno^h, F. Yuanⁱ, T. Meixner^j, A. Bytnerowicz^a

^a US Forest Service, Pacific Southwest Research Station, 4955 Canyon Crest Drive, Riverside, CA 92507, United States

^b Center for Conservation Biology, University of California, Riverside, CA 92521, United States

^c Department of Botany and Plant Sciences, University of California, Riverside, CA 92521, United States

^d Creekside Center for Earth Observations, Menlo Park, CA, United States

^e US Forest Service, Pacific Northwest Research Station, 620 SW Main Suite 400, Portland, OR 97205, United States

^f US Forest Service, Pacific Northwest Air Resource Management Program, P.O. Box 1148, Corvallis, OR 97339, United States

^g Center for Environmental Research and Technology, Bourns College of Engineering, University of California, Riverside, CA 92521, United States

^h Ecotoxicology of Air Pollution, CIEMAT (Ed. 70), Avda. Complutense 22, 28040 Madrid, Spain

ⁱ Institute of Arctic Biology, University of Alaska Fairbanks, 902 Koyukuk Drive, Fairbanks, AK 99775, United States

^j Department of Hydrology and Water Resources, University of Arizona, Tucson, AZ 85721, United States

ARTICLE INFO

Article history:

Received 2 November 2009

Received in revised form

23 June 2010

Accepted 19 July 2010

Available online 11 August 2010

Keywords:

Critical loads

California ecosystems

Nitrogen deposition

Eutrophication

Nitrogen response thresholds

Air pollution effects

Management options

Grassland

Coastal sage scrub

Desert

Pinyon-juniper

Forest

Chaparral

Oak woodland

Epiphytic lichens

ABSTRACT

Empirical critical loads for N deposition effects and maps showing areas projected to be in exceedance of the critical load (CL) are given for seven major vegetation types in California. Thirty-five percent of the land area for these vegetation types (99,639 km²) is estimated to be in excess of the N CL. Low CL values (3–8 kg N ha⁻¹ yr⁻¹) were determined for mixed conifer forests, chaparral and oak woodlands due to highly N-sensitive biota (lichens) and N-poor or low biomass vegetation in the case of coastal sage scrub (CSS), annual grassland, and desert scrub vegetation. At these N deposition critical loads the latter three ecosystem types are at risk of major vegetation type change because N enrichment favors invasion by exotic annual grasses. Fifty-four and forty-four percent of the area for CSS and grasslands are in exceedance of the CL for invasive grasses, while 53 and 41% of the chaparral and oak woodland areas are in exceedance of the CL for impacts on epiphytic lichen communities. Approximately 30% of the desert (based on invasive grasses and increased fire risk) and mixed conifer forest (based on lichen community changes) areas are in exceedance of the CL. These ecosystems are generally located further from emissions sources than many grasslands or CSS areas. By comparison, only 3–15% of the forested and chaparral land areas are estimated to be in exceedance of the NO₃ leaching CL. The CL for incipient N saturation in mixed conifer forest catchments was 17 kg N ha⁻¹ yr⁻¹. In 10% of the CL exceedance areas for all seven vegetation types combined, the CL is exceeded by at least 10 kg N ha⁻¹ yr⁻¹, and in 27% of the exceedance areas the CL is exceeded by at least 5 kg N ha⁻¹ yr⁻¹. Management strategies for mitigating the effects of excess N are based on reducing N emissions and reducing site N capital through approaches such as biomass removal and prescribed fire or control of invasive grasses by mowing, selective herbicides, weeding or domestic animal grazing. Ultimately, decreases in N deposition are needed for long-term ecosystem protection and sustainability, and this is the only strategy that will protect epiphytic lichen communities.

Published by Elsevier Ltd.

1. Introduction

An estimated land area of 52,823 km² of California (13% of the state) is exposed to N deposition greater than 10 kg ha⁻¹ yr⁻¹ (Fig. 1).

A significant portion of the Central Valley, and montane sites in the SW Sierra Nevada, and in southern California receive deposition inputs ranging from 15 to 20 kg ha⁻¹ yr⁻¹ or greater (Fig. 1; Fenn et al., 2008). Forests in the more exposed regions of southern California experience the highest N deposition in North America (30 to over 70 kg ha⁻¹ yr⁻¹), while at the opposite end of the deposition spectrum in California large acreages of forests, woodlands, shrublands, grasslands, desert, high elevation ecosystems, and other ecosystem

* Corresponding author. Tel.: +1 951 680 1565; fax: +1 951 680 1501.

E-mail address: mfenn@fs.fed.us (M.E. Fenn).

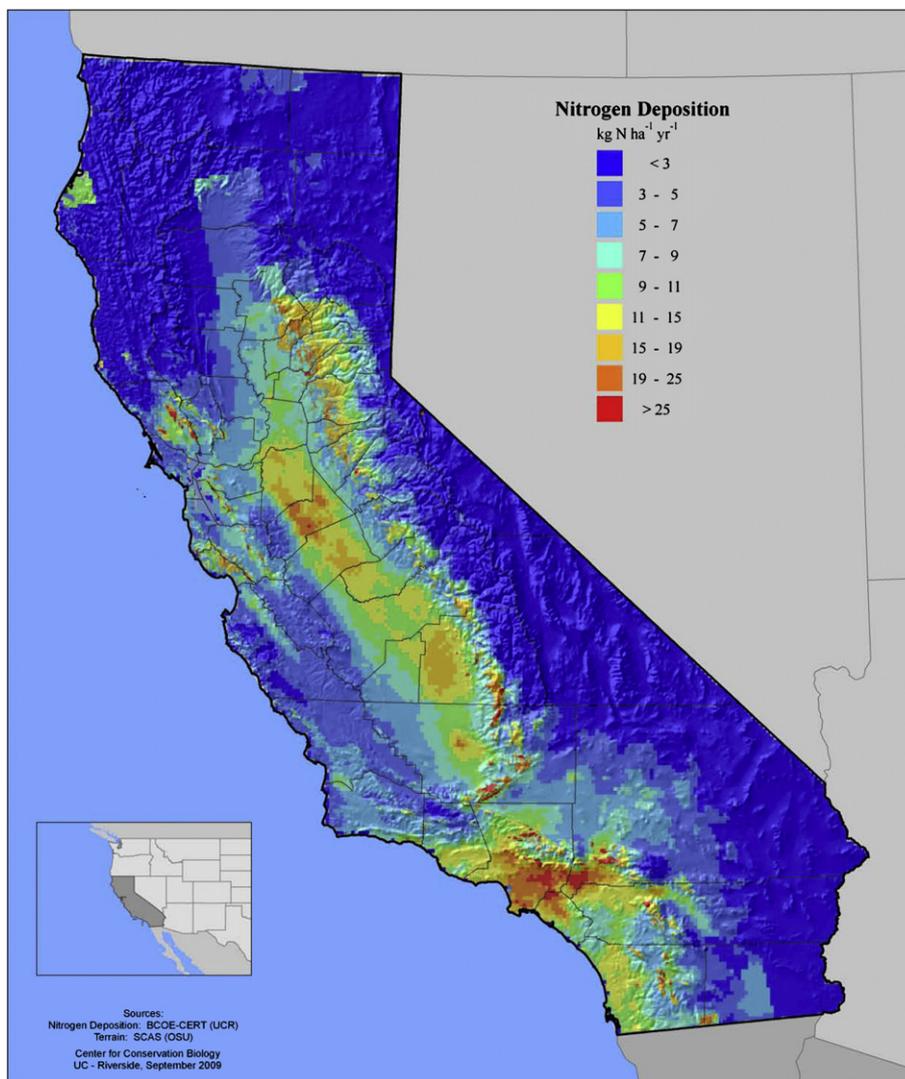


Fig. 1. Map of total annual N deposition in California based on CMAQ simulations. As described in the text, simulated N deposition in forested areas has been adjusted based on the linear relationship with empirical throughfall data.

types are exposed to low deposition (ca. 2–5 kg ha⁻¹ yr⁻¹; Fig. 1; Fenn et al., 2003a, 2008).

Nitrogen emissions in California are 3–10 times greater than in the other ten western states (Fenn et al., 2003a). Emission estimates are more uncertain for ammonia (NH₃) than for nitrogen oxides (NO_x), but available data suggest that NH₃ comprises 20–30% of N emissions in California (Cox et al., 2009; Fenn et al., 2003a; USEPA, 2008). A recent study found that 25% of the N emissions from light-duty vehicles in three California cities are in the form of NH₃ and in newer cars this fraction increases (Bishop et al., 2010). Nitrogen deposition studies (Fenn and Poth, 2004; Fenn et al., 2003a, 2008) and monitoring networks of gaseous pollutants (Bytnerowicz et al., 2007; Hunsaker et al., 2007) suggest that NH₃ emissions in California are underestimated. Satellite observations of atmospheric NH₃ also show that concentrations are greater than previous data indicated in several regions of the world, including central and southern California (Clarisse et al., 2009). Emissions of NH₃ appear to be increasing as NO_x emissions decrease (Cox et al., 2009; Fenn et al., 2003a).

Eighty-six percent of NO_x emissions in California are from mobile sources and 11% from stationary sources. The largest source of NH₃ emissions is livestock waste, estimated as approximately 80% of the

statewide emissions by the California Air Resources Board (Cox et al., 2009). However, as discussed above, on-road emissions appear to be a more important source of NH₃ emissions than the emissions inventories indicate (Bishop et al., 2010), particularly in urban areas (Battye et al., 2003) or near highways (Fig. 2). In montane and desert regions downwind of greater Los Angeles and in the Central Valley of

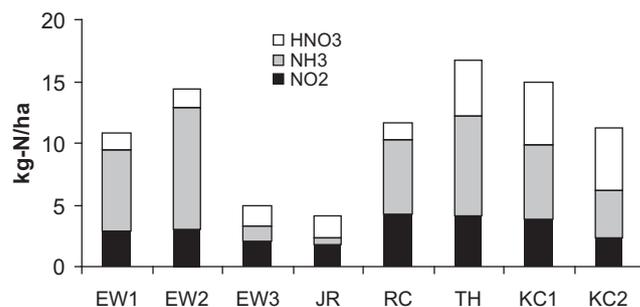


Fig. 2. Passive sampler estimates of dry gaseous deposition at serpentine grassland sites. The Edgewood sites (EW) are from a local gradient adjacent to Highway 280. From these sites the critical load was derived.

California, N deposition and atmospheric concentrations of gaseous pollutants have similar or even higher proportions of reduced than oxidized N (A. Bytnerowicz, unpublished data; Fenn and Poth, 2004; Fenn et al., 2003a, 2008).

Until recently, little was known regarding the thresholds at which various ecosystems in California are impacted by chronic N deposition or the geographic extent of these impacts (Weiss, 2006). Herein we review our current understanding of the empirical critical loads (CLs) of N deposition at which undesirable effects are observed for seven of the most extensive vegetation types in California. A critical load (CL) has been defined as: “A quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge” (UBA, 2004).

Affected vegetation communities include mixed conifer forests, chaparral, oak woodlands, coastal sage scrub, grasslands, pinyon-juniper, and desert ecosystems (Fig. 3). The land cover distribution shown in Fig. 3 represents potential natural vegetation before urbanization and modern agriculture (U.S. Bureau of Reclamation, 1996). A number of biotic communities and ecosystem components and processes are known to be affected by these chronic N inputs, and empirical CLs have been established for key endpoints.

Predominant effects are those associated with excess N or the CL for ‘N as a nutrient’ effects ($CL_{nut}(N)$; Reynolds et al., 1998; UBA, 2004). Soils in these Mediterranean ecosystems are typically high in base saturation and are well buffered, thus tolerating the acidification impacts caused by chronic N deposition. However soil base saturation and pH have decreased significantly in forests and chaparral sites in the Los Angeles air basin where N deposition is $\geq 25 \text{ kg ha}^{-1}$ (Breiner et al., 2007; Fenn et al., 1996; Wood et al., 2007).

Critical loads for terrestrial systems can be calculated from models of varying complexity and are determined for eutrophication or nutrient N effects as well as for soil acidification (UBA, 2004). Models for the latter also include acidification effects from sulfur deposition. In California, sulfur deposition is rarely of concern and N eutrophication effects are much more widespread than acidification effects, particularly in terrestrial ecosystems in California. In this study we focus on empirically derived CLs for ‘N as a nutrient’ effects. Much of this work is based on data collected at sites across N deposition gradients or from N amendment studies.

The primary objectives of this report are to provide a synthesis of empirical CLs for N across major vegetation types in California and to look for spatial patterns and the extent of CL exceedances. The empirical CL values given in this paper include previously

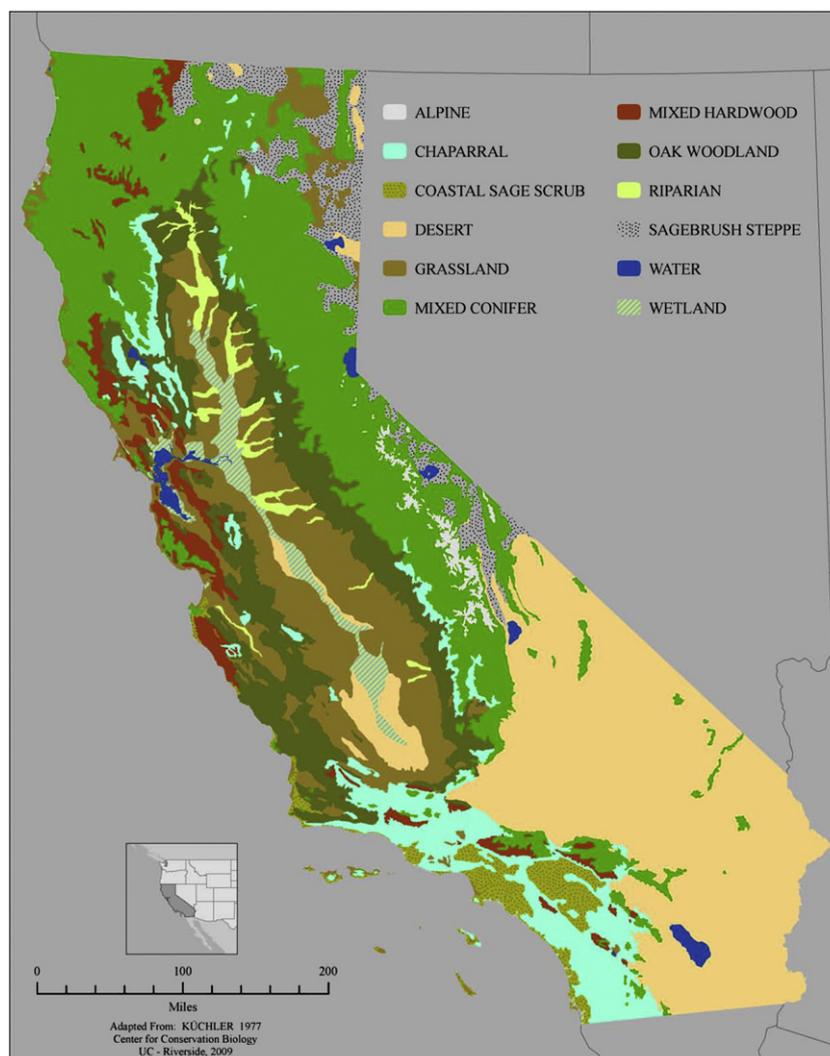


Fig. 3. Map of the distribution of vegetation types and land cover in California (U.S. Bureau of Reclamation, 1996). Land cover presented in this figure represents potential natural vegetation before urbanization and modern agricultural development.

published CLs and newly established CLs, most of which are also reported in a comprehensive monograph on N CLs in the U.S. (Pardo et al., in press). This assessment will provide a broad-scale assessment of the geographic extent over which ecosystems in California are at risk of deleterious ecological effects from N deposition and will serve as a guide for future research in key vegetation types. Finally, management options for mitigating the effects of excess N in these vegetation types are discussed.

2. Materials and methods

A variety of methods were used to measure N deposition and to determine the CLs for the seven vegetation types discussed in this paper. Methods for determining the CL were adapted based on the sensitive responders to chronic N deposition within each vegetation type and measured or simulated N deposition. Finally, CL exceedance areas were mapped by overlaying statewide vegetation maps with a California N deposition map (Tonnesen et al., 2007).

2.1. N deposition

Because of the importance of dry deposition in California and the difficulty in measuring dry deposition, particularly to shrublands, several approaches (Fenn et al., 2009) were used to estimate total annual N deposition inputs in the different vegetation types evaluated in this study. In some cases a combination of methods was used for a given vegetation type. Throughfall deposition data were used to determine the CLs in forest and chaparral ecosystems (Fenn et al., 2003a, 2008; Meixner and Fenn, 2004). Simulated deposition data from the USEPA CMAQ (Models-3/Community Multiscale Air Quality) model (Byun and Schere, 2006; Tonnesen et al., 2007) were used for chaparral and oak woodlands in the Central Valley, for coastal sage scrub, and for broad scale estimates of deposition to grassland. The CMAQ model is designed to represent both wet and dry deposition of aerosol and gas-phase species. However, the CL for serpentine grassland was based on local scale deposition in the environs of a major highway as determined using the inferential method (Fenn et al., 2009) for dry deposition, combined with estimates of wet and particulate deposition. Atmospheric concentrations of NO₂ (Ogawa, 1998), NH₃ (Roadman et al., 2003) and HNO₃ (Bytnerowicz et al., 2005) were measured in the grassland with passive samplers (Fenn et al., 2009) that were deployed along a deposition transect. Deposition data for desert vegetation in Joshua Tree National Park were determined from a combination of CMAQ simulations, bulk deposition and

throughfall measurements. The CMAQ deposition data in the desert were confirmed by inferential deposition calculations determined from passive sampler data (A. Bytnerowicz and M.E. Fenn, unpublished data). Throughfall and bulk deposition samples collected in forest, chaparral and desert vegetation were obtained using ion exchange resin samplers (Fenn and Poth, 2004; Fenn et al., 2009).

2.2. Empirical critical load determinations

Critical loads within each of the vegetation types were determined based on the responses of biological or chemical response variables to varying levels of N inputs. These response variables include epiphytic lichen community changes, elevated streamwater nitrate leaching, reduced biodiversity of native plant species, invasion of exotic grass species, and changes in mycorrhizal communities. When more than one response variable was used within a given vegetation type, a CL was estimated for each response variable. Low productivity ecosystems respond to low levels of N by changes in plant species composition and productivity (Bowman et al., 2006; Allen et al., 2009), while high productivity ecosystems may not show changes in species composition even with relatively high N inputs, but may experience detectable changes in soil or streamwater chemistry (Fenn and Poth, 1999; Fenn et al., 1996, 2003c). However, epiphytic lichen communities in high production ecosystems can respond to low N levels (Fenn et al., 2007, 2008; Jovan, 2008; Jovan and McCune, 2005).

2.2.1. Mixed conifer forest, chaparral and oak woodlands

Empirical CLs in mixed conifer forests were determined for elevated streamwater NO₃⁻ concentrations and shifts in epiphytic lichen community functional groups. A preliminary CL was also determined for reductions in fine root biomass in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.; Fenn et al., 2008; Table 1). Responses to N have also been reported for increased bark beetle activity and associated tree mortality (Jones et al., 2004), changes in ectomycorrhizal fungal communities (Sirajuddin, 2009), understory biodiversity (Allen et al., 2007), and soil acidification (Breiner et al., 2007; Wood et al., 2007) but further studies are needed to determine more certain estimates of the CLs for these effects. Similar approaches to that used for forests were employed to determine the CLs for elevated NO₃⁻ leaching in streamwater and epiphytic lichen community changes in chaparral and oak woodlands (Table 1; Fenn et al., 2003a–c, in press; Fenn and Poth, 1999; Meixner and Fenn, 2004; Riggan et al., 1985).

Table 1

Summary of CLs and methods used to determine empirical CLs for the 7 vegetation types described in this study.

Vegetation type	Response variables for CL determination	CL values (kg N ha ⁻¹ yr ⁻¹)	References
Mixed conifer forest	Exceedance of peak streamwater NO ₃ ⁻ concentration threshold (0.2 mg NO ₃ -NL ⁻¹)	17	Fenn et al., 2008
Mixed conifer forest	Enriched N in tissue of the lichen <i>Letharia vulpina</i> (above 1.0% N)	3.1	Fenn et al., 2008
Mixed conifer forest	Epiphytic lichen community shift away from acidophyte (oligotroph) dominance	5.2	Fenn et al., 2008
Mixed conifer forest	Extirpation of acidophytic (oligotrophic) lichens	10.2	Fenn et al., 2008
Mixed conifer forest	Fine root biomass reduction (26%) in ponderosa pine trees	17	Fenn et al., 2008
Chaparral	Exceedance of peak streamwater NO ₃ ⁻ concentration threshold	10–14	Fenn et al., in press
Chaparral and oak woodlands	Epiphytic lichen community shift to eutrophic lichen species dominance	5.5	Fenn et al., in press; Jovan, 2008; Jovan and McCune, 2005
Coastal sage scrub	Decrease in native plant species and forb richness	7.8–10	Fenn et al., in press
Coastal sage scrub	Decrease in arbuscular mycorrhizal spore density, richness, and percent root infection	10	Fenn et al., in press
Grassland	Exotic grass invasion	6	Weiss, 1999; This study
Desert scrub	Exotic grass biomass accumulation sufficient to sustain fire	3.2–9.3	Rao et al., 2010
Pinyon-juniper woodland	Exotic grass biomass accumulation sufficient to sustain fire	3.0–6.3	Rao et al., 2010

2.2.2. Coastal sage scrub

Critical loads have been estimated for coastal sage scrub (CSS) vegetation with respect to loss of diversity of native plants and diversity of mycorrhizal fungi. Elevated N may also increase exotic grass biomass that may be responsible for frequent fires. CSS is a semi-deciduous shrubland that occurs in the Mediterranean-type climate of southern and central coastal California, extending southward to Baja California, Mexico. The understory forbs, primarily annual, are especially high in diversity, with many species of concern throughout the range of CSS in California. Coastal sage scrub is subject to N deposition levels of approximately $20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (estimated total N deposition from the CMAQ model; Tonnesen et al., 2007) in inland Riverside and San Bernardino Counties, where it has been rapidly converted to exotic annual grassland in the past 30–40 years (Allen et al., 1998; Talluto and Suding, 2008). The conversion to grassland is likely caused by a combination of elevated N deposition that promotes increased grass biomass and frequent fire, which in turn prevents establishment of native shrubs and forbs (Allen et al., 1998; Minnich and Dezzani, 1998). Coincident with increasing exotic grass cover is the loss of native diversity. The CL approach taken here was to determine a threshold N deposition at which there is a distinct decline in native species diversity. To this end a survey was done in 2003 along an N deposition gradient in CSS with an estimated deposition range of $8.7\text{--}19 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, according to the CMAQ model (Tonnesen et al., 2007). The inferential method (Fenn et al., 2009) yielded a corroborating range estimate of $6.6\text{--}20.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Because measurements for the inferential method were taken at only three points, both modeled and measured values are used to set the CL.

Another analysis was done along the same gradient to determine the N CL for effects on colonization and diversity of arbuscular mycorrhizal fungi (AMF) in CSS (Egerton-Warburton and Allen, 2000; Fenn et al., in press). AMF are found in the roots of most plant species, and are important mutualists that promote plant growth. High levels of nutrients such as N decrease the percentage of roots colonized by AMF and decrease the number of spores found in the rhizosphere (Egerton-Warburton and Allen, 2000; Egerton-Warburton et al., 2007). The CL for AMF responses in CSS was based on a steep decline in mycorrhizal root infection and spore species density at the second lowest, compared to the lowest, level of N deposition observed across the N deposition gradient (Fenn et al., in press).

2.2.3. Grassland

In the San Francisco Bay Area, nutrient-poor soils derived from serpentinite bedrock support diverse grassland, dominated by native herbs and perennial grasses that produce spectacular spring wildflower displays. Most California grasslands on richer soils are dominated by non-native annual grasses and herbs. Serpentine grasslands provide a refuge for imperiled native California grassland flora and fauna (Harrison and Viers, 2007), including the federally “Threatened” Bay checkerspot butterfly (*Euphydryas editha bayensis*) and more than 10 rare, threatened, and endangered plant taxa (USFWS, 1998). The Bay checkerspot butterfly and serpentine grasslands have been intensively studied since the 1960s, and are recognized as model systems for population, conservation, and ecosystem ecology (Huenneke et al., 1990; Hobbs and Mooney, 1995; Ehrlich and Haanski, 2004).

The only remaining viable population complex of the butterfly occupies approximately 2000 ha of serpentine grassland around the southern Santa Clara Valley, just downwind of the San Francisco–San Jose urban agglomeration. N deposition from urban emissions allows non-native annual grasses, especially *Lolium multiflorum* and *Bromus hordeaceus*, to vigorously invade serpentine soils and displace the native herbs, including the checkerspot larval host plants (*Plantago erecta* and *Castilleja* sp.) and numerous adult nectar sources (Weiss,

1999). Short-term experimental studies, using 100 or more kg N ha^{-1} have demonstrated that N is the limiting nutrient for annual grass growth in these soils (Huenneke et al., 1990; Hull and Mooney, 1990). Increased grass growth and accumulation of undecomposed litter lead to losses of larval host plants and adult nectar sources, and local population extinctions of the butterfly.

On the coastal San Francisco Peninsula, upwind of most pollution sources, serpentine grasslands have remained relatively free of vigorous grass invasions, except at Edgewood Natural Preserve (EW) adjacent to Highway 280, an 8-lane high speed road carrying 100,000+ vehicles/day in a relatively clean air region. In this 15 ha habitat the local Bay checkerspot population declined from 5000 in 1997 to zero in 2002. During this period, a wave of *L. multiflorum* over-ran larval host plants up to about 400 m east from the road, leading to the loss of 80% of the available habitat.

A monitoring network of passive samplers (Fenn et al., 2009) in serpentine grassland provided monthly average atmospheric concentrations of NO_2 , NH_3 , and HNO_3 from which dry deposition estimates for these gases were calculated using published deposition velocities. Wet deposition from CMAQ is estimated at a maximum of $0.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. Dry particulate deposition is estimated at $<0.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Blanchard et al., 1996). The CL for invasion of exotic annual grasses was determined at the Edgewood Natural Preserve along a transect from highly traveled Highway 280. The EW3 air monitoring station was deliberately placed where the grass invasion visibly diminished (as of 2001).

2.2.4. Desert

Nitrogen fertilization was applied at four sites along an N deposition gradient in Joshua Tree National Park (JTNP). Fertilization rates were 0, 5 and $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, applied for three consecutive years from 2003 to 2005 as pelleted NH_4NO_3 (Allen et al., 2009). Nitrogen deposition along the gradient ranged from 3.4 to $12.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ as measured by bulk throughfall deposition samplers (Fenn et al., 2009) and also as simulated with the CMAQ model (Tonnesen et al., 2007). Highly similar values for dry deposition (the predominant input form) were determined with the inferential method (Rao et al., 2009). The fertilization plots were in two vegetation types, creosote bush scrub in the Colorado Desert portion of JTNP, and pinyon-juniper woodland in the Mojave Desert. The two vegetation types represent two of the most abundant vegetation types in JTNP, as well as the extremes in elevation. Creosote bush scrub is also the most abundant vegetation type across the Mojave and Sonoran Deserts. The sites have been invaded by exotic annual grasses, especially *Schismus barbatus* and *Bromus madritensis*, both of which are highly responsive to N fertilizer. The empirical CL was determined as the lowest N treatment plus background N deposition that caused increased biomass of invasive grasses and decreasing biomass of native species (Allen et al., 2009).

Critical loads were also determined for creosote bush scrub and pinyon-juniper woodlands by simulating winter annual vegetation production under a range of soil textures, precipitation regimes, and N deposition levels. Simulations were conducted using the biogeochemical process model DayCent, and are described in detail in Rao et al. (2010). Briefly, the model was calibrated and validated using soil and vegetation data from the four fertilization sites in JTNP described above and in Allen et al. (2009). Once parameterized for each vegetation type, DayCent was used to simulate winter annual biomass production under increasing N deposition loads from background ($1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) to twice the level observed in this region ($15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$). Production was simulated for 100 years at each N deposition load, and the fire risk at each load determined as the fraction of years in which the threshold of biomass known to carry fire ($1000 \text{ kg N ha}^{-1}$) was exceeded. When fire risk probability was plotted as a function of increasing N deposition, a sigmoidal

response curve was obtained. The lower-bound CL was then defined as the N deposition load where fire risk began increasing exponentially above background levels. The amount of N deposition where fire risk no longer increased with added N was termed the fire risk stabilization load and was defined as the amount of N deposition resulting in 90% of the maximum fire risk. In regions with deposition above this load, fire risk is controlled by variation in annual precipitation and does not increase with increased N deposition, although annual biomass production will still increase with added N (Rao et al., 2010). These calculations were conducted for simulations performed under six precipitation regimes and six soil textures. The ranges of precipitation and soil textures included in the simulations bracketed observed mean annual precipitation and soil texture from the southern California desert region.

2.3. Critical load exceedance maps

Vegetation cover data from the California Gap Analysis Project (Davis et al., 1998) were overlain with statewide CMAQ total annual N deposition data to create maps showing the areas in which estimated N deposition is in excess of the CL values reported in this study. Urban and agricultural land use categories were excluded from this process of developing CL exceedance maps. Environmental Systems Research Institute (ESRI, Redlands, California) ArcGIS desktop version 9.3 software was used for spatial analysis and to produce CL exceedance maps. The CL exceedance map series are based on vegetation cover extant circa 1992 (Davis et al., 1998). These data include a classification using the California Wildlife Habitat Relationships (WHR) system (Mayer and Laudenslayer, 1988). Selected WHR classes were aggregated to match the CL vegetation types presented here.

Nitrogen deposition was converted from a raster to a polygon format then overlaid and intersected with vegetation cover. This produced a polygon dataset and table, including each type and area of vegetation with its associated N deposition. Vegetation polygons that included areas with varying annual N deposition values were partitioned into areas with the appropriate deposition value associated with each new area. Each vegetation type was categorized by N deposition to determine CL exceedance areas, which were then symbolized accordingly on the CL exceedance maps. The sum of all areas in exceedance of the CL was calculated for each vegetation cover. The N deposition and CL exceedance maps are displayed showing county boundaries and shaded relief for improved spatial recognition.

Simulated N deposition was calculated for the most polluted two-thirds of the state on a 4-km resolution grid (Tonnesen et al., 2007). The relatively unpolluted regions in northern California to the north of a line extending from Mendocino on the coast to Doyle on the California/Nevada border and in the far southeastern corner of the state (east of a line from Pahrump, Nevada to El Centro, California) were simulated on a 36-km grid resolution and merged with the 4-km simulation to produce a statewide N deposition map (Fig. 1) that was used to develop the CL exceedance maps. Previous results show that the 36 km grid does not estimate deposition in high pollution sites in California as well as the 4-km grid simulations, but performs well in less polluted regions (Fenn et al., 2003a; M.E. Fenn, unpublished data). The CL exceedance maps provide estimates of the areal extent for high potential of undesirable effects from excess nutrient N for each of the seven vegetation types.

3. Results and discussion

3.1. Mixed conifer forest critical loads

The N CL for incipient NO_3^- leaching was estimated at $17 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ from regression analysis of peak concentrations of

NO_3^- in streamwater runoff versus throughfall N deposition. A CL for a 26% reduction in fine root biomass was also estimated to be $17 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ from regression analysis of previously published fine root biomass data (Grulke et al., 1998) and throughfall data (Fenn et al., 2008). Enhanced N accumulation in lichen material and shifts in lichen community functional groups were the most sensitive responders to atmospheric N deposition. An empirical CL of $3.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ was calculated for enhanced lichen tissue N concentrations, which corresponded with the initiation of community changes (Fenn et al., 2008). At a throughfall N deposition level of $5.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ the lichen community shifted from acidophyte dominance to neutrophyte dominance. Lichen species classified as acidophytes were extirpated at a CL of $10.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Fenn et al., 2008).

3.2. Chaparral and oak woodlands critical loads

In chaparral ecosystems empirical CLs have been estimated for NO_3^- in streamwater of small catchments (4–10 ha) with rapid ephemeral runoff responses following precipitation. A higher CL is estimated as catchments increase in size because of greater capacity to retain and process atmospherically deposited N within the terrestrial and riparian portions of the catchment. Intermediate sized catchments (30–150 ha) commonly receive NO_3^- largely from groundwater exfiltration in addition to ephemeral NO_3^- inputs from surface runoff. Large catchments (>150 ha) have a greater N retention capacity due to in-stream N uptake processes and groundwater–surface water interactions at larger scales and thus have lower streamwater NO_3^- concentrations than intermediate sized catchments (Meixner and Fenn, 2004). Nonetheless, because of insufficient data to further differentiate the CL based on catchment characteristics, the estimated CL is the same for intermediate and large catchments considering that NO_3^- concentrations are above the critical threshold ($0.2 \text{ mg NO}_3\text{-N L}^{-1}$ or $14.3 \text{ }\mu\text{M}$) in both instances when N deposition exceeds the CL of $14 \text{ kg ha}^{-1} \text{ yr}^{-1}$. The CL determined for small “flashy” catchments (4–10 ha) is set at $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, based on long-term streamwater NO_3^- data from Chamise Creek in Sequoia National Park (Fenn et al., 2003b,c) and throughfall data from Ash Mountain (Fenn et al., 2003a) located 4 km to the west of Chamise Creek. This low NO_3^- leaching CL is believed to be a result of leaching of N accumulated from deposition to soil and plant surfaces, or through stimulation of nitrification or both mechanisms (Fenn et al., 2003c). The estimated CL of $14 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for intermediate and large chaparral catchments is based on data from eight catchments in the Devil Canyon region of the western San Bernardino Mountains (Fenn and Poth, 1999; Meixner and Fenn, 2004). Based on the sparsity of N-saturated chaparral catchments in the SW Sierra Nevada where N deposition is often greater than $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$ and a survey of chaparral catchments in southern California (Riggan et al., 1985), it appears that this higher N CL ($14 \text{ kg ha}^{-1} \text{ yr}^{-1}$) for NO_3^- leaching is more common and applicable over a greater geographic area than the small catchment CL of $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$.

The calculated CL for effects on epiphytic lichen communities in oak woodlands and chaparral regions of the Central Valley of California, the surrounding central Coast Ranges, and Sierra foothills (lichen data from Jovan and McCune, 2005) was highly similar to that of mixed conifer forests as described above. The CL for the shift to nitrophyte dominance in the lichen community was estimated to be $5.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Fenn et al., in press).

3.3. Coastal sage scrub critical loads

Extractable soil N ($\text{NO}_3^- + \text{NH}_4^+$) ranged from $10 \text{ }\mu\text{g g}^{-1}$ at the rural end of a N deposition gradient, to $39 \text{ }\mu\text{g g}^{-1}$ at the urban end.

Percent cover of exotic grasses was positively correlated with soil N (Padgett et al., 1999) and atmospheric deposition, while cover of native shrubs and forbs was inversely correlated. Across sites spanning this gradient from low to high N deposition, total species richness ranged from 92 to 34 per 3 ha parcel surveyed, and, of these, 67 to 16, respectively, were native forb species (Choi et al., 2008; E. Allen, Unpubl.; Fenn et al., in press). Sites were chosen that had not burned for ten years so they would be in a similar successional stage. However, high deposition sites (13.4–19.6 kg N ha⁻¹ yr⁻¹ from CMAQ estimates; Tonnesen et al., 2007) have a history of two or more fires since the 1960s, while the moderately low deposition sites (8–11 kg N ha⁻¹ yr⁻¹) burned only once since the 1960s. A rapid drop in native species cover and forb richness was observed between 9 and 11 kg N ha⁻¹ yr⁻¹, so 10 kg N ha⁻¹ yr⁻¹ may be estimated as the CL for loss of native diversity and cover. Using N estimates from the inferential method (Fenn et al., in press), the rapid drop occurred between 6.6 and 8.9 kg N ha⁻¹ yr⁻¹, making the intermediate value 7.8 kg N ha⁻¹ yr⁻¹ the CL for a decline in native species. Because of the uncertainty in the modeled vs. the values calculated with the inferential method, we use two CLs, 7.8 and 10, for CSS vegetation.

An analysis of mycorrhizal spores along the CSS gradient showed spore density and root colonization declined logarithmically, with 10 kg N ha⁻¹ yr⁻¹ as the CMAQ-determined CL (Egerton-Warburton and Allen, 2000; Allen, unpubl.) and thus 7.8 kg N ha⁻¹ yr⁻¹ from the inferential method. Spore density declined from 110 g⁻¹ to 50 g⁻¹ soil, while colonization ranged from 45 to 15% of root length from low (8.7 kg ha⁻¹ yr⁻¹) to high (19.6 kg ha⁻¹ yr⁻¹) N deposition, respectively. There was also a loss of species richness, declining from 19 to 12 spore morphotypes, although this was a monotonic decline and no CL could be determined. The spore density, richness, and percent colonization values from the sites with lowest N deposition (8 kg ha⁻¹ yr⁻¹) were similar to values found in cleaner areas in the region (Sigüenza et al., 2006b). It is noteworthy that the CL for both CSS vegetation (exotic grass cover, native forb richness) and AMF (root colonization, spore density) were the same. The mechanism for this may be that as N increases, the highly mutualistic native species decline and are replaced by grasses that are less dependent on mycorrhizae (Sigüenza et al., 2006a).

3.4. Grassland critical loads

Within the grassland monitoring network in the San Francisco/San Jose area TH, KC1 and KC2 are south San Francisco Bay sites where grass invasions have consistently occurred and deposition exceeds 10 kg N ha⁻¹ yr⁻¹ (Figs. 2 and 4a,b). At the opposite end of the deposition spectrum, site JR receives 4 kg N ha⁻¹ yr⁻¹, and grass invasions have been minimal compared with TH and KC. The three sites at Edgewood (EW1, 35 m west of Highway 280, EW2 35 m east of the road, and EW3 367 m east of EW2) provide a fine-scale N dry-deposition gradient from >15 kg N ha⁻¹ yr⁻¹ at EW2 to 5 kg N ha⁻¹ yr⁻¹ at EW3. EW3 is the site where the grass invasion is greatly diminished, and thus used to establish the CL for annual grass invasion of 5 kg N ha⁻¹ yr⁻¹ as dry deposition (Fig. 2). Including an upper bound of 1 kg N ha⁻¹ yr⁻¹ from wet and particulate deposition increases the critical load to 6 kg N ha⁻¹ yr⁻¹. This CL is similar to the lower end of estimates for sensitive European grasslands (Bobbink and Roelofs, 1995) and for Minnesota prairie grasslands (Clark and Tilman, 2008).

Deposition across the localized EW gradient is dominated by NH₃ from 3-way catalytic converters that were introduced around 1990 (Baum et al., 2001; Durbin et al., 2002; Fraser and Cass, 1998; Kean et al., 2000). Deposition from HNO₃ is much lower than from NH₃ at the EW and JR sites because of clean oceanic air during the

warm season when HNO₃ concentrations are highest. All urban and near urban sites have high levels of NH₃ deposition (Fig. 2).

The N CL for prairie grasslands in Minnesota, USA was established based on chronic low-level N additions (Clark and Tilman, 2008). The lowest N treatment level was 10 kg ha⁻¹ yr⁻¹ at a site with an estimated 6 kg ha⁻¹ yr⁻¹ of ambient N deposition. From a simple regression model the CL for significant reductions in species number was estimated to be 5.3 kg ha⁻¹ yr⁻¹, virtually identical to our CL for serpentine grassland near San Jose, California. The time required to detect consistent reductions in species varied from three to nine years when N amendments ranged from 10 to 95 kg ha⁻¹ yr⁻¹ (Clark and Tilman, 2008). Thus, given sufficient time, relatively low N deposition inputs can impact species biodiversity. Clark and Tilman (2008) concluded that long-term studies using high rates of N addition may poorly predict, and even underestimate, the impact of chronic low rates of N deposition.

The only well-defined CL for California grasslands is that for serpentine grasslands as presented herein. Nitrogen addition studies in California grasslands have caused invasions by exotic species and other species diversity impacts, but N addition levels (50–100 kg N ha⁻¹ yr⁻¹) were too high to determine the N CL (Huenneke et al., 1990; Maron and Jefferies, 1999; Zavaleta et al., 2003). Further studies using low levels of chronic N amendments and space for time studies are needed to evaluate the CL for California grasslands. However, we hypothesize that the CL for many California grasslands will likely fall within the 5–10 kg N ha⁻¹ yr⁻¹ range based on grassland CL studies elsewhere (Bobbink et al., 2010; Clark and Tilman, 2008), our serpentine grassland CL, and previous N fertilization studies in California grasslands.

3.5. Desert critical loads

In the N fertilization experiment in Joshua Tree National Park there were few vegetation biomass responses the first year, 2003; some responses the second year, 2004, which had moderate precipitation; and more responses in a record wet year, 2005. Invasive grasses increased under both 5 and 30 kg N ha⁻¹ fertilizer additions at two of four sites in 2005. One of these was a pinyon-juniper woodland with the highest level of N deposition, and the other was creosote bush scrub with the lowest level of N deposition. In a drier year, only 30 kg ha⁻¹ caused an increase in invasive grasses in two of the four sites. Thus 8 kg ha⁻¹ yr⁻¹ (5 kg ha⁻¹ added + 3 kg ha⁻¹ background deposition) can be considered the empirical CL for increased invasive grasses in a wet year. Native forbs decreased at sites with increased grass response to N, but at sites with naturally low grass invasion, native forbs responded positively to added N at 5 kg ha⁻¹. The surprisingly high response of plants to N in the low deposition creosote bush scrub site may be because it has the lowest rock cover of all the sites. The sandy soil is highly suitable for colonization by invasive grasses with fine roots. Even though the latter site is remote with good air quality, it has a high cover of exotic grasses in wet years. Thus N deposition will interact with soil texture to determine the N CL, and relatively small amounts of N input will promote invasive grass growth in soils with low rock and gravel content. A soil map of the desert will help in a mapping effort to determine which sites will be most susceptible to exotic annual grass invasion where N deposition exceeds 8 kg ha⁻¹ yr⁻¹.

Exotic annual grass invasion is a concern in the desert because these grasses compete with native annuals leading to a loss of diversity and vegetation-type conversion. Another concern of vegetation-type conversion is the increase in fine fuel that promotes fire. Deserts seldom have sufficient fuel for fire, but fires have become more frequent in some areas of the California Mojave and Sonoran deserts (Brooks et al., 2004; Brooks and Matchett, 2006). Under N deposition and higher than average rainfall, some areas of

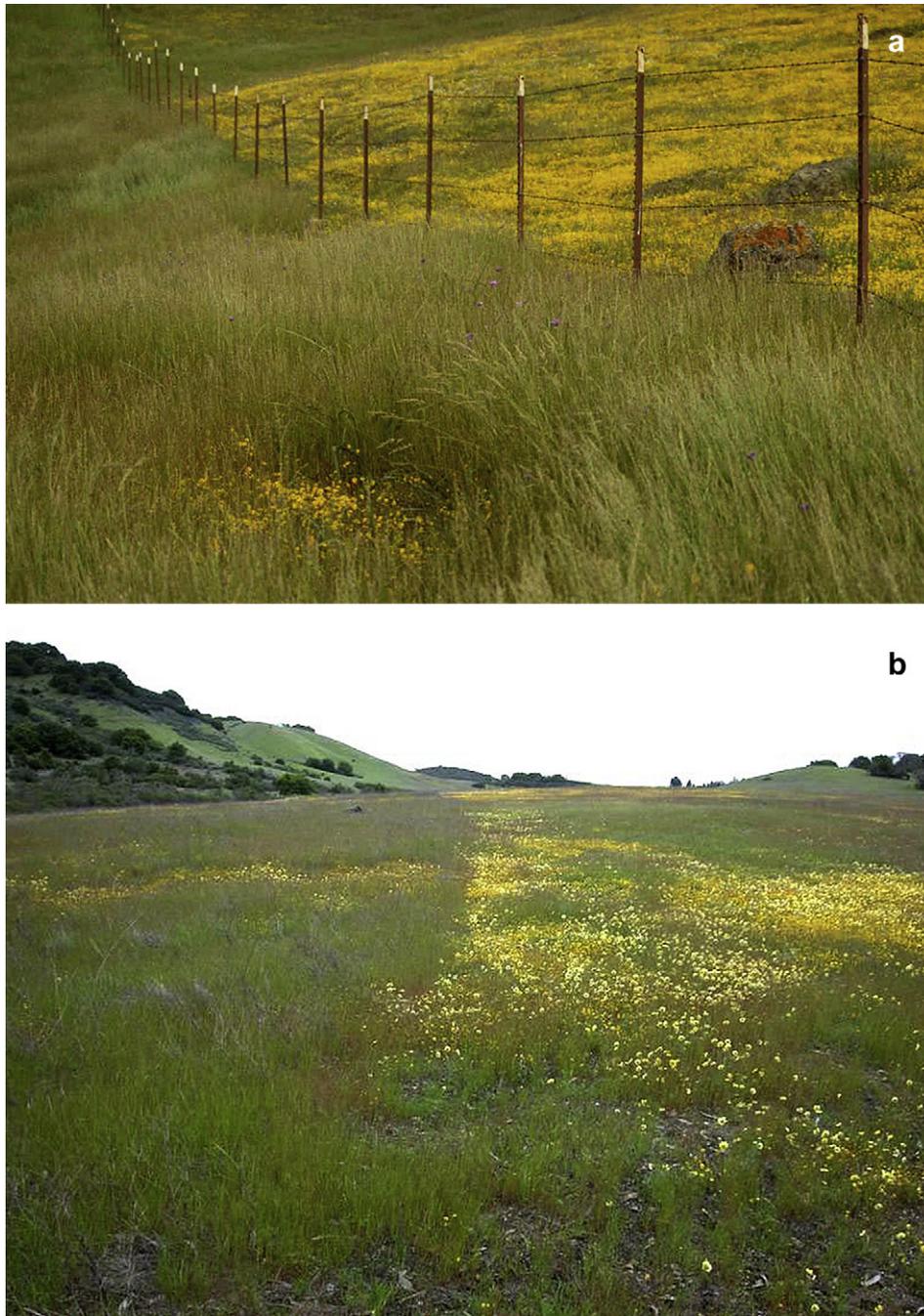


Fig. 4. (a) Site KC1 on the left side of the fence is ungrazed. Deposition at this site is estimated at $15 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ as determined from the passive sampler data and $10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ from the 36-km grid CMAQ simulations (Weiss, 2006). (b) The effect of a May 2005 mowing (right side) in a grassland is seen in April 2006.

these deserts have been burning frequently (Brooks, 2003; Brooks and Matchett, 2006). The fuel level needed to carry a fire is about 1000 kg ha^{-1} of continuous dry grass cover (Scifres and Hamilton, 1993). This amount of fuel was produced in the fertilized shrub interspaces during the 2005 wet year, but also in the high N deposition range of the N gradient where fires have been occurring in the last two decades (Rao and Allen, 2010; Rao et al., 2010).

Using the biogeochemical model DayCent, the risk of exceeding the fire threshold was calculated for both pinyon-juniper woodland and creosote bush scrub. The model results indicate that many areas of CA deserts are above the CL, which was defined as the N load at which fire risk began to increase exponentially. Above the

CLs of these ecosystems, small increases in N deposition result in large increases in fire risk, up to the fire risk stabilization load. Using the creosote bush scrub fire stabilization load, modeled for eight soil textures and four precipitation regimes representative of creosote bush habitat in the state (Rao et al., 2010), we calculated the average fire risk stabilization load at $8.15 \text{ kg ha}^{-1} \text{ yr}^{-1}$. This value is very similar to the empirical CL for creosote bush determined from the fertilization experiment discussed at the beginning of this section, suggesting that this level of N deposition will be detrimental to both diversity and fire dynamics.

The pinyon-juniper woodland areas are more likely to burn than creosote bush scrub due to the greater abundance of woody

biomass (Brooks and Minnich, 2006). In addition, most pinyon-juniper woodlands are in areas with greater average precipitation than creosote bush scrub (Rowlands, 1995), resulting in reduced water limitation for the winter annuals that are the fine fuel allowing fire to carry between trees and shrubs. Thus, the CL and the fire stabilization load for pinyon-juniper were lower than in creosote bush scrub. The low N deposition levels that result in increased fire risk in pinyon-juniper woodlands indicates that much of this ecosystem type in California is at high risk of fire due to the combination of increased fine fuel production from deposition and inherently high woody fuel abundance. In summary, the empirical CL for exotic grass invasion in desert ecosystems is $8 \text{ kg ha}^{-1} \text{ yr}^{-1}$. The range including the lower and upper bounds of the CL for creosote bush scrub and pinyon-juniper woodlands are 3.2–9.3 and $3.0\text{--}6.3 \text{ kg ha}^{-1} \text{ yr}^{-1}$, respectively based on fire risk probability from DayCent simulations (Table 1; Rao et al., 2010).

3.6. Comparison to critical loads in Europe and the rest of the US

Mediterranean systems are reportedly prone to N loss with chronic N deposition because of actively nitrifying soils and major precipitation and runoff in winter (Fenn et al., 1998). However, recent studies show only incipient low-level NO_3^- losses in streamwater in California forests at a CL of $17 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Fenn et al., 2008). Similarly, in an oak forest in Spain no NO_3^- loss was observed with N deposition of $15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Ávila et al., 2002, Rodà et al., 2002). By comparison, the CL for NO_3^- leaching in temperate forests in the NE United States is $8 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Aber et al., 2003). Stoddard et al. (2001) reported that for catchments within the ICP Waters network in Europe and North America at stage 2 of N saturation, (episodic elevated NO_3^- and high base-flow NO_3^- during the growing season), the average N deposition was only $14 \text{ kg ha}^{-1} \text{ yr}^{-1}$. This is a much more advanced stage of NO_3^- loss than that observed in California forests at the CL of $17 \text{ kg ha}^{-1} \text{ yr}^{-1}$.

These comparisons indicate that Mediterranean forests are actually less prone to NO_3^- leaching than temperate catchments. The comparatively low NO_3^- export in Mediterranean catchments when expressed as annual N mass loss (e.g., kg N ha^{-1}) is certainly due to the high evapotranspiration and low precipitation surplus in Mediterranean watersheds. However, NO_3^- concentrations in runoff can be as high as 300–400 μmolar during peak runoff events, and isotopic studies in southern California show that 20–40% of NO_3^- in runoff during storm events is direct throughput of unassimilated atmospheric NO_3^- (Michalski et al., 2004). In summary, forest and to a lesser extent, chaparral watersheds in California, and possibly other Mediterranean regions appear to have higher CLs for NO_3^- leaching loss compared to temperate forests. At the same time, catchments in California may be more prone to experience direct throughput of atmospheric N without biological assimilation when the CL is exceeded. Furthermore, small chaparral catchments ($\leq 10 \text{ ha}$) at low elevation with low N retention capacity can have CLs as low as $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$, similar to that in other ecoregions.

In Europe the empirical CL range for lichen communities in temperate and boreal forests is $10\text{--}15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Bobbink et al., 2003). However, this may be overestimated, presumably as a result of observations at sites already impacted by ambient N deposition; true low N deposition control sites no longer exist in much of Europe. Recent studies suggest that a more appropriate CL range for lichen community effects in Europe and North America is $3\text{--}10 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (De Vries et al., 2007; Nordin et al., 2005; Van Dobben et al., 2006; Pardo et al., in press), with CLs tending toward the high end at sites with greater precipitation (Geiser et al., 2010). By comparison, the N CL at which epiphytic lichen communities in California forest and chaparral/oak woodland ecosystems shift from oligotrophic to eutrophic dominance is

$5.2\text{--}5.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Fenn et al., 2008; Pardo et al., in press). Early declines in oligotrophic lichens can be detected at $3 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in coniferous forests of the Sierras and northwestern CA (Pardo et al., in press).

No CLs are available for Mediterranean shrublands in other regions to compare to the CSS CLs in California. The N CL given for serpentine and other grasslands in California in this study ($6 \text{ kg ha}^{-1} \text{ yr}^{-1}$) is on the low end of the range of CLs proposed for grasslands in Europe and North America. Estimated CLs for tall-grass prairie is $5\text{--}15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ and $10\text{--}25 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for mixed- and short-grass prairie (Clark, in press). In Europe the CL range for three grassland vegetation classes including xeric, semi-arid and Mediterranean grasslands is given as $10\text{--}25 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Bobbink et al., 2003; R. Bobbink, personal communication). More research is needed in all these grassland types, but the available evidence suggests that California grasslands may be among the most sensitive to N deposition. This is presumably a result of the high invasive pressure from exotic grass species in California, which thrive under conditions of increased N availability.

We are not aware of studies in deserts to determine CL outside of the US, but tentative CLs can be estimated from studies in other US deserts. For instance, there was no productivity response by desert grassland in New Mexico to N deposition of $5.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$, but there was an increase with N fertilization of $20 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Baez et al., 2007). The researchers concluded that the CL lies between these two values. In Idaho cold desert, fertilization of $6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ caused a depletion in soil moisture, that was likely related to increased sagebrush production. Because there was no recharge of soil moisture in subsequent years, this has a potential for affecting future plant production negatively (Inouye, 2006). A higher level of fertilization of $12 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ caused no greater response, so $6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ may be a CL, or nearly so. However, the site receives $1.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ wet deposition as measured at a nearby NADP station, but total wet plus dry deposition is unknown. These values for biotic responses to N deposition (Baez et al., 2007; Inouye, 2006) are in the range of $3\text{--}9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ expected to cause increased productivity of herbaceous vegetation based on the DayCent model and N fertilization studies (Allen et al., 2009; Rao and Allen, 2010; Rao et al., 2010).

3.7. Critical load exceedances in California

For every vegetation type included in this study a large proportion of the land area is in excess of the CL, with values ranging from 29 to 54% of the land area exceeding the CL (Table 2). This is not surprising considering that the CL is $3\text{--}8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for lichen community changes in forests, chaparral and oak woodlands and for plant community changes in desert and grasslands as a result of annual grass invasions. In descending order, the vegetation types with the highest percent land cover in exceedance of the CL are: coastal sage scrub > chaparral (lichen effects) > grassland > oak woodland > desert scrub > pinyon-juniper > mixed conifer forest (lichen effects) > chaparral (NO_3^- leaching) > mixed conifer forest (NO_3^- leaching) (Table 2). When comparing the vegetation types in terms of absolute area (km^2) in exceedance, the descending order of CL exceedance (using the lowest available CL values for each vegetation type) is: mixed conifer forest (lichen effects) > desert scrub > chaparral (lichen effects) > oak woodland > grassland > mixed conifer forest (NO_3^- leaching) > chaparral (NO_3^- leaching) > coastal sage scrub > pinyon-juniper. The spatial patterns and extent of CL exceedance for the seven vegetation types are shown in Figs. 5–11.

Coastal sage scrub and annual grasslands had high percent in exceedance (54 and 44%; Table 2) which may be attributed to the low estimated CLs of 6 and $7.8 \text{ kg ha}^{-1} \text{ yr}^{-1}$, and also that these

Table 2Areal extent (km²) and percent land area in exceedance of the CL for seven vegetation types in California^a.

Vegetation cover and CL basis	Area of vegetation cover	Lowest CL value (kg N ha ⁻¹ yr ⁻¹)	Low CL exceedance area	Percent exceedance	Highest CL value (kg N ha ⁻¹ yr ⁻¹)	High CL exceedance area	Percent exceedance
Coastal sage scrub (invasives)	6328	7.8	3396	53.7	10.0	2098	33.2
Chaparral (lichen community effects)	27,045	5.5	14,315	52.9	5.5	14,315	52.9
Annual grassland (invasives)	28,634	6.0	12,496	43.6	7.5	8795	30.7
Oak woodland (lichen community effects)	32,659	5.5	13,454	41.2	5.5	13,454	41.2
Desert scrub (fire risk)	75,007	3.2	23,369	31.2	9.3	439	0.6
Pinyon-juniper (fire risk)	6602	3.0	2013	30.5	6.3	1386	21.0
Mixed conifer forest (lichen community effects)	106,663	3.1	30,596	28.7	5.2	24,998	23.4
Chaparral (nitrate leaching) ^b		10.0	3947	14.6	14.0	891	3.3
Mixed conifer forest (nitrate leaching)		17.0	4754	4.5			
Summary of 7 vegetation types	282,938		99,639 ^c	35.2 ^c		65,485 ^c	23.1 ^c

^a For coastal sage scrub, annual grassland, desert scrub, pinyon-juniper, mixed conifer forests (lichen community effects), and chaparral (NO₃ leaching) vegetation types a low and high CL value were used to determine the areal extent of CL exceedances for each of these vegetation types. Only one CL value was calculated for lichen community effects in chaparral and oak woodlands and for NO₃ leaching in mixed conifer forest. See text for details.

^b The lower CL for NO₃ leaching in chaparral applies to small catchments (e.g., 4–10 ha) and the high CL for larger catchments. See text for details.

^c In these summary CL exceedance calculations only the lichen CLs were used for the chaparral and forest vegetation types; the NO₃ leaching CL data were not used for these summaries. In determining the high CL exceedance area and percent land area in exceedance for the summary of the seven combined vegetation types, the highest CL value was used when more than one CL was established. However, since only one CL was determined for lichen community effects in chaparral and oak woodland, the same CL and CL exceedance areas were used for the lowest and highest CL exceedance calculations.

vegetation types are concentrated at low elevation sites near population or agricultural centers (Figs. 2, 8 and 9). Likewise, 53% of the chaparral area (low to moderate elevation habitats) was in exceedance of the CL for lichen community changes, a sensitive responder to N deposition. Four additional vegetation types had exceedance areas of 29–41% (Table 2). These can be attributed to the relatively low CL values (3.0–5.5 kg ha⁻¹ yr⁻¹) for lichen community shifts in oak woodlands and mixed conifer forests, and for fire risk to the low biomass desert scrub or pinyon-juniper systems. In contrast, we estimated that 5 and 15% of the forest and

chaparral (low-end CL of 10 kg ha⁻¹ yr⁻¹) areas are in exceedance of the NO₃ leaching CL (Table 2). When the high-end CL for NO₃ leaching in chaparral (14 kg ha⁻¹ yr⁻¹) is considered only 3.3% of the chaparral area is in exceedance. The exceedance of the CL for NO₃ leaching in forests and chaparral is a less widespread problem than the vegetation or lichen community changes observed.

Combining the exceedance areas of the seven vegetation types results in an estimated 99,639 km² in exceedance of the N CL in California, which equals 35% of the land area of the included vegetation types (Fig. 12a; Table 2). In these exceedance areas,

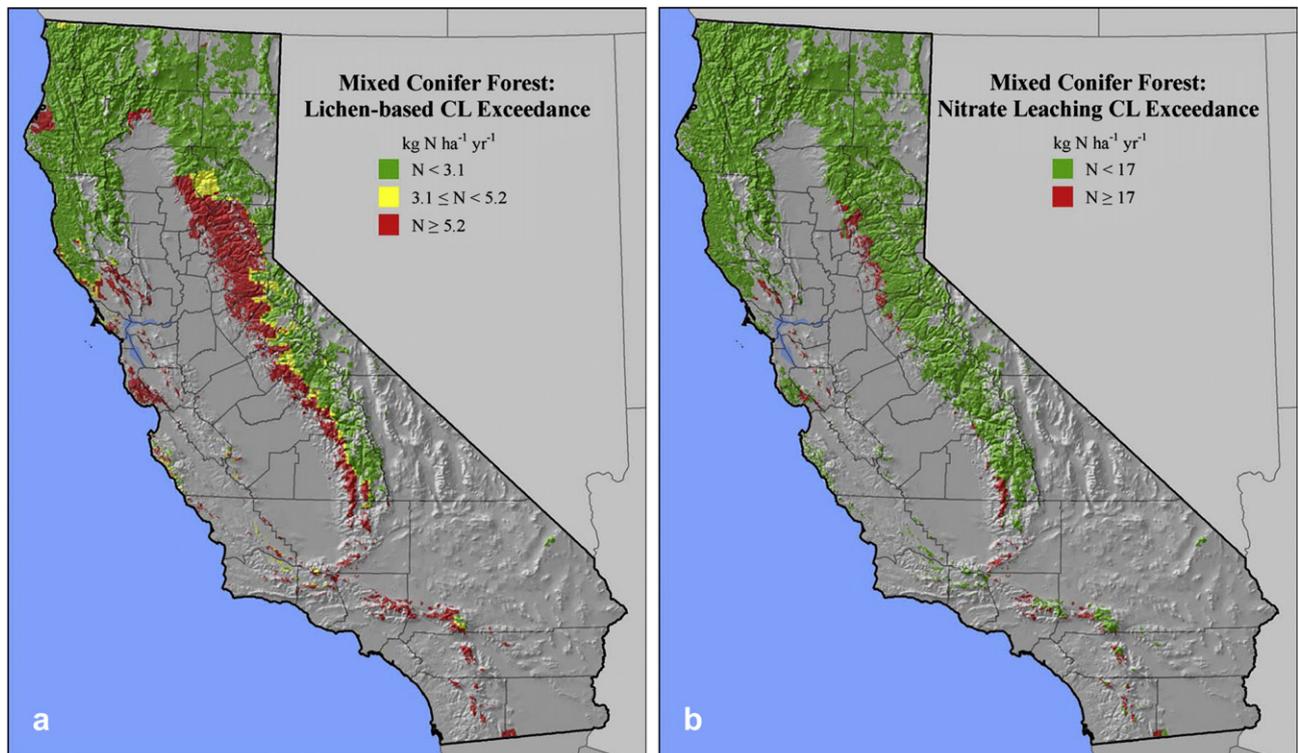


Fig. 5. Critical load exceedance map for mixed conifer forests based on (a) lichen community effects and (b) nitrate leaching.

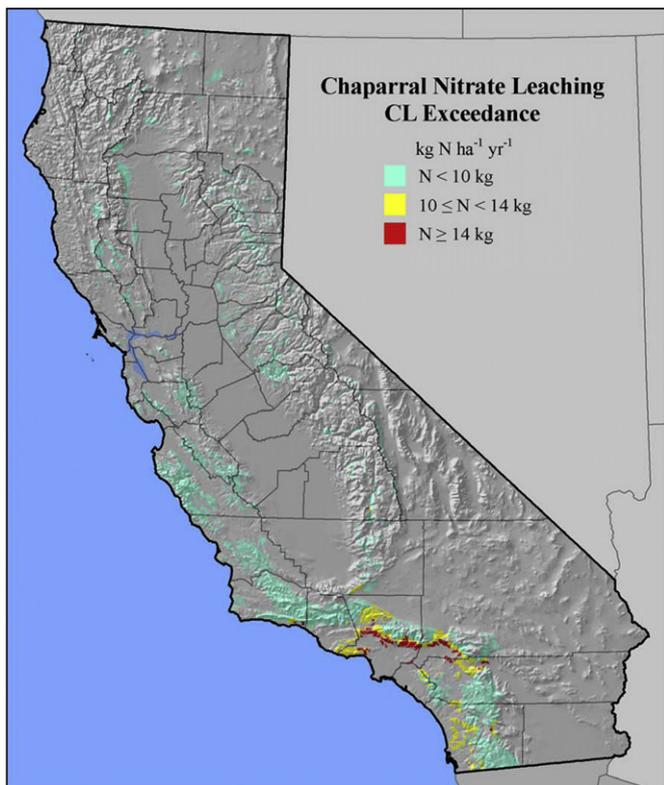


Fig. 6. Critical load exceedance map for chaparral ecosystems showing areas in exceedance of a low-end (yellow) and high-end (red) nitrate leaching critical load.

grasslands, desert and CSS ecosystems are at risk of type conversion as a result of invasion by exotic annual grasses, a dramatic effect and fundamental ecosystem change. In desert and CSS the increased fuel accumulation from invasive grasses greatly increases the risk of fire danger, and fire strongly favors vegetation-type conversion. This is particularly problematic in the desert where fires are normally rare and as a result native vegetation is threatened, particularly in wet years when biomass production potential is much greater (Rao et al., 2010; Rao and Allen, 2010). In forests, chaparral and oak woodlands lichen communities undergo dramatic community changes as a result of N deposition in exceedance of the CL. The lichen CL can serve as an early warning signal to identify areas where initial N effects are occurring and where additional impacts may be observed now or in the future (Fenn et al., 2008). In forests downwind of urban areas in southern California lichen community changes occurred decades ago (Nash and Sigal, 1999), many probably in the first half of the twentieth century (Fenn et al., 2008).

Fig. 12a,b shows the level of CL exceedance statewide, including all seven vegetation types, for the low- and high-end CL estimates. The low-end CLs are exceeded by at least $5 \text{ kg ha}^{-1} \text{ yr}^{-1}$ over approximately 27% of the exceedance area and by at least $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$ in 10% of the exceedance area (Fig. 12a). When considering the high-end CL exceedance areas, regions that are no longer in exceedance include much of the desert in the southeast, the eastern Sierra Nevada, portions of the western edge of the Central Valley and western central California (Fig. 12b). These exceedance maps indicate that N deposition needs to be reduced by $5\text{--}15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ or more over much of the western foothills of the Sierra Nevada, the mountains of the SW Sierra Nevada and the Transverse Ranges of southern California.

The exceedance areas do not necessarily represent areas where the effects upon which the CL is based have already occurred,

although in many instances this is predominantly the case (e.g., lichen effects and NO_3^- leaching). Most conservatively, these can be considered areas where the estimated N deposition is at or above the CL at which these effects have been documented for this vegetation type. Exceedance areas represent sites at elevated risk of negative impacts from N excess. Factors that may influence whether undesirable impacts from N deposition actually occur within a site include site and land use and management history; soil, climatic and topographic conditions; species composition; and site disturbances. With the exception of clear lichen community effects from N deposition, critical loads based on plant physiological or plant community responses may be more uncertain than those based on chemical criterion (e.g., NO_3^- leaching), even though the latter are controlled by biological and nutrient cycling processes. For example, Vourlitis and Pasquini (2009) found that N fertilizer addition to CSS vegetation in plots characterized by a dense shrub canopy caused changes in the relative abundance of dominant shrubs, but not herbaceous plant species. This is in contrast to the effects of decades-long N deposition in CSS stands with a more open structure, resulting in exotic annual grass invasion as reported herein.

Preliminary data from the San Bernardino Mountains downwind from greater Los Angeles indicate that the CL for increased NO_3^- leaching in mixed conifer forests is also associated with a 26% reduction in root biomass in ponderosa pine (Fenn et al., 2008). Although this and other biological and ecophysiological N deposition effects are less well quantified, current information from mixed conifer forests in California suggests that NO_3^- leaching or N saturation symptoms in general are indicative of biological effects such as altered tree physiology, root:shoot ratios, and susceptibility to pests (Fenn et al., 2003c; Grulke et al., 1998; Jones et al., 2004). Nitrate leaching CL exceedance areas may also be areas where forest health and sustainability are at greater risk, but these quantitative relationships require further development. In Europe

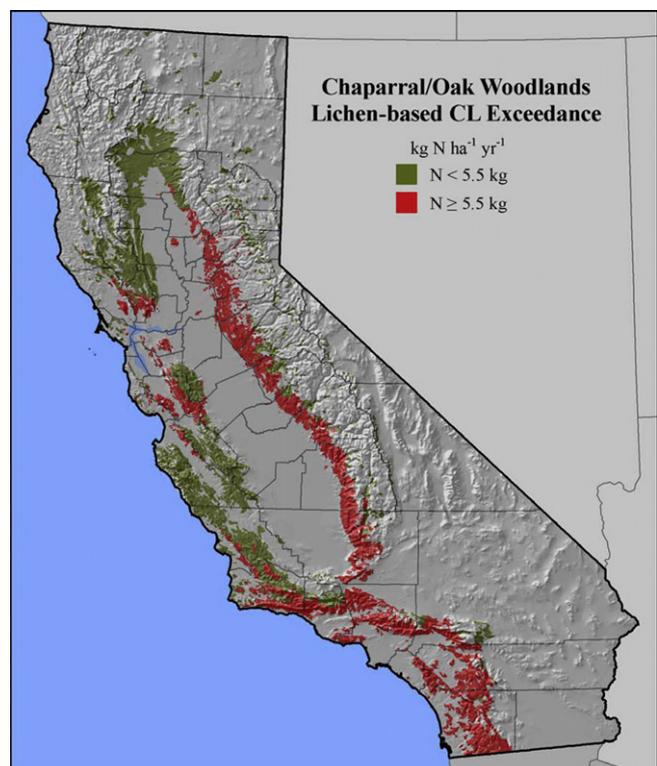


Fig. 7. Critical load exceedance map for chaparral and oak woodlands showing areas in exceedance of the critical load for effects on epiphytic lichen communities.

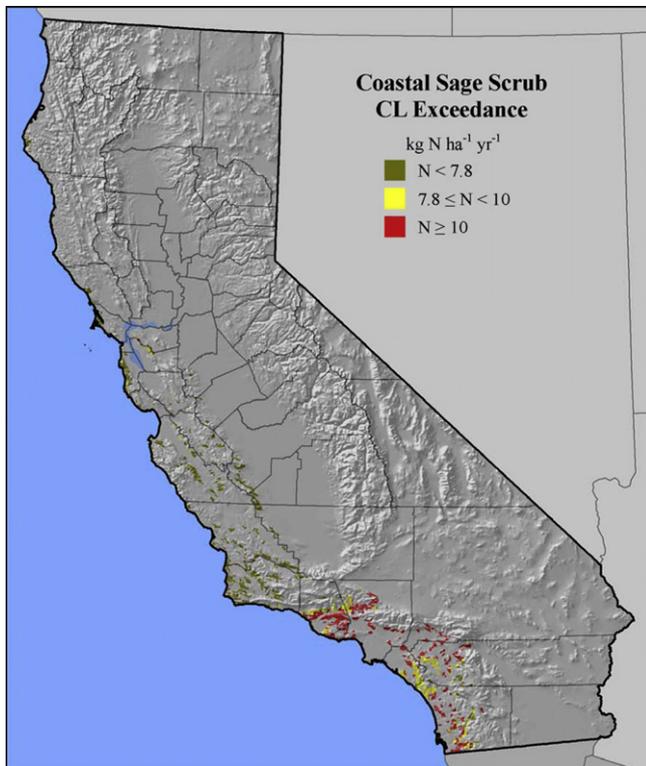


Fig. 8. Critical load exceedance map for coastal sage scrub showing exceedance of the critical load for plant and mycorrhizal community changes.

attempts have been made to relate NO_3^- concentrations in soil leachate to effects on forests and plant function in order to use these relationships to set empirical CLs (De Vries et al., 2007). The documented combined effects of ozone and N deposition in mixed conifer forests contribute to a syndrome of greater drought stress, susceptibility to bark beetle attack, tree mortality and increased fire occurrence (Grulke et al., 2009; Jones et al., 2004). Thus, in forests, as shown for CSS, desert and grasslands in California, N deposition at sufficient dose can contribute to dramatic changes in vegetation structure.

3.8. Uncertainty in critical loads and exceedance maps

The main sources of uncertainty associated with the CL exceedance maps are from the simulated estimates of N deposition and the extrapolation of the CL from the study sites where the empirical CL was determined to the statewide occurrence of the vegetation type. Thus, the CL exceedance maps are based on the assumption that the CL for a given vegetation is similar throughout the state. We consider that the empirical CL exceedance maps are likely to represent areas at risk for N excess effects more effectively than broad scale CL maps based on computed steady-state simple mass balance CLs, which are only tenuously related to actual observations of structural or functional changes in terrestrial ecosystems influenced by N deposition. Furthermore, the computed CLs are based on highly uncertain input parameters and outputs has been much discussed in the literature (Cresser, 2000; De Vries et al., 2007; Heywood et al., 2006; Rodriguez-Lado et al., 2007; UBA, 2004).

While the empirical CLs are expected to reflect biological responses to excess N more accurately than soil-based CL models for nutrient N (De Vries et al., 2007; Fenn et al., 2008), the CL exceedance maps also entail uncertainty associated with errors in simulating N deposition inputs with CMAQ. However on a statewide basis

simulation modeling is the only way to estimate N deposition and it provides a uniform method for estimating deposition across vegetation types. We compared throughfall N deposition at 26 forested sites in the Sierra Nevada and San Bernardino Mountains with CMAQ estimates. There was reasonable agreement when throughfall deposition was $\leq 6\text{--}7 \text{ kg ha}^{-1} \text{ yr}^{-1}$ but as N deposition increased CMAQ underestimated N deposition. However a significant linear relationship was found between CMAQ deposition and throughfall N deposition ($y = -12.20 + 4.34x$; $r^2 = 0.80$). The CMAQ underestimates for forests may be due to inadequate capability to model orographic effects on pollutant transport and deposition in montane sites. Thus, in preparing the statewide N deposition map and the CL exceedance maps we adjusted CMAQ deposition for the forested sites based on the linear relationship with the empirical throughfall data.

The lichen-based CLs for forests and chaparral/oak woodlands and the forest NO_3^- leaching CL are considered robust because they are based on data from a large area representative of these vegetation types (Fenn et al., 2008, in press; Jovan, 2008; Jovan and McCune, 2005). The CSS CL is based on a regional N deposition gradient and fertilization experiments in southern California; however the CL could be overestimated because of the lack of a true low N control site within the study region (Fenn et al., in press). The chaparral NO_3^- leaching CL is primarily based on chaparral catchments in Sequoia National Park and the western San Bernardino Mountains.

The desert CL is based on fertilization experiments and biogeochemical modeling (Rao et al., 2010) in two desert types (Mojave and Colorado) within Joshua Tree National Park. The average CL for each vegetation type was determined as the break from low to intermediate fire risk, and was calculated as the average from the model runs for all soil types and the precipitation

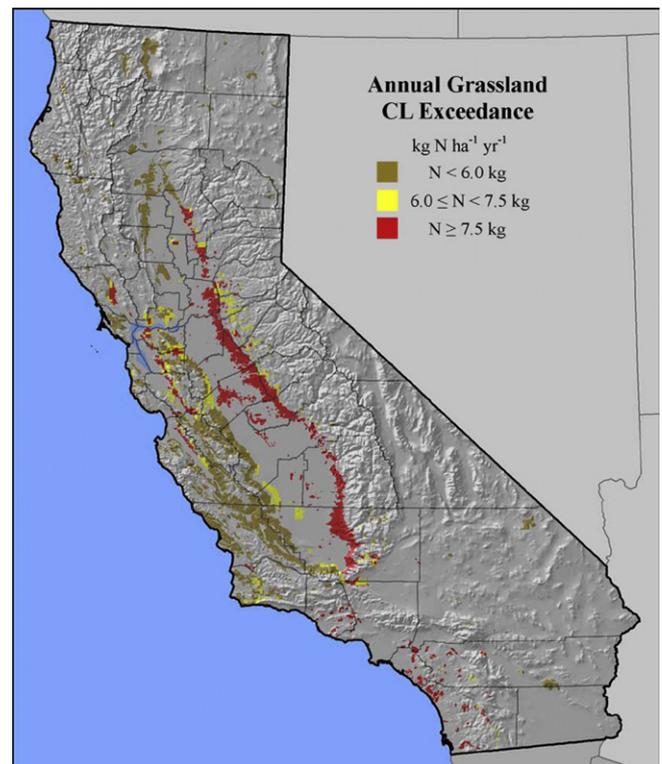


Fig. 9. Critical load exceedance map for annual grassland showing exceedance of the critical load for plant community changes. The CL for grassland ($6.0 \text{ kg ha}^{-1} \text{ yr}^{-1}$) is based on a roadside gradient study in serpentine grassland. Because of the uncertainty in extrapolating this CL to other grasslands, the CL exceedance for a CL of $7.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$ is also presented.

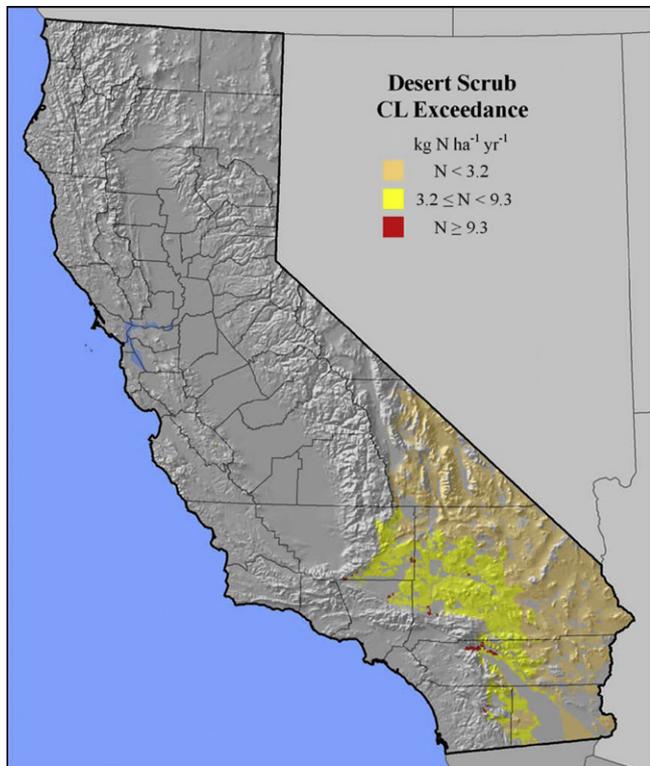


Fig. 10. Critical load exceedance map for desert scrub showing exceedance of the critical load for plant community changes.

regimes most common for that vegetation type (creosote bush scrub $n = 24$; pinyon-juniper $n = 12$). The break from intermediate to high fire risk was defined as the N deposition load where fire risk stabilized, and was similarly averaged across soil types and precipitation for each vegetation type.

The extrapolation for CL exceedances may be more uncertain for grassland because the CL is based only on serpentine grassland (Harrison and Viers, 2007; Weiss, 1999). However, the CL for serpentine grassland in California ($6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) is similar to that estimated for Minnesota prairie grassland ($5.3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; Clark and Tilman, 2008). We also consider the serpentine grassland CL as a reasonable, but possibly a conservative estimate for California grasslands, considering studies suggesting that serpentine grasslands are less responsive to added N than other California grasslands and are also less prone to exotic invasions (Harrison and Viers, 2007). Many N addition studies have shown the responsiveness of California grasslands to added N but the N treatments have been too high to determine the threshold response level or CL (Harpole et al., 2007; Huenneke et al., 1990; Zavaleta et al., 2003). Furthermore, grassland studies from other regions of North America and Europe also suggest that low levels of N deposition can cause significant biodiversity impacts as N accumulates in the ecosystem (Bobbink et al., 2010; Clark and Tilman, 2008; Stevens et al., 2004). Because of the lack of N response studies in California grasslands at N addition levels approximating the putative N CL, we will present the geographic distribution of potential exceedance by using the serpentine-based CL value of 6 as well as a more conservative value of $7.5 \text{ kg N ha}^{-1} \text{ yr}^{-1}$.

3.9. Potential effects of climate change on critical loads in California

Another uncertainty in determining N CLs is the effect of climate change. Rockström et al. (2009) describe three earth-system

processes that due to anthropogenic activities have already surpassed boundaries that are considered safe for the planet's continued ability to support human life; these are climate change, rate of biodiversity loss, and interference with the N cycle. Likewise, in California all three of these interrelated environmental threats are of concern. Temperatures in California are projected to increase by $1.5\text{--}4.5 \text{ }^\circ\text{C}$ by the end of the century under the various IPCC emissions scenarios (Cayan et al., 2008). Relatively small (less than approximately 10%) changes in overall precipitation are projected for California (Cayan et al., 2008), but climate models and trends project more frequent and longer lasting extreme storm events in North America (CCSP, 2008) and California (Bromirski and Flick, 2008). Climate warming is projected to reduce snow accumulation in California because more precipitation is expected to fall as rain and less as snow. A larger proportion of the streamflow volume will occur earlier in the year, and in snowmelt driven basins late winter snowpack accumulation is projected to decrease by 50% toward the end of this century (Miller et al., 2003). Low elevation catchments that are not dominated by snowmelt runoff but where runoff is largely controlled by vegetation water demand (e.g., chaparral), will likely experience decreased runoff as evapotranspiration rates increase (Tague et al., 2009).

If the future climate in California is characterized by more severe droughts interspersed with increased occurrence of extreme precipitation events, this is likely to have a strong influence on the dynamics of N accumulation and N fluxes, which in turn will affect CL values. In theory, such scenarios would result in lower N CLs because N is expected to accumulate in catchments during successive dry years followed by greater susceptibility to NO_3^- leaching and N volatilization losses in high precipitation years. It is unclear how these kinds of scenarios will affect plant N availability and the CL for effects on plants. In a warmer climate, the N CL for NO_3^- leaching in chaparral catchments may increase as runoff

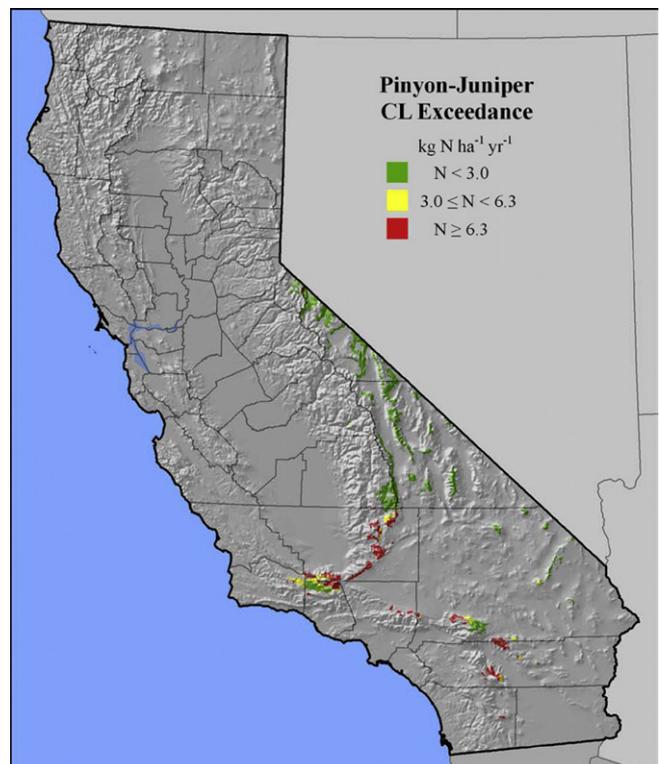


Fig. 11. Critical load exceedance map for pinyon-juniper vegetation showing exceedance of the critical load for plant community changes.

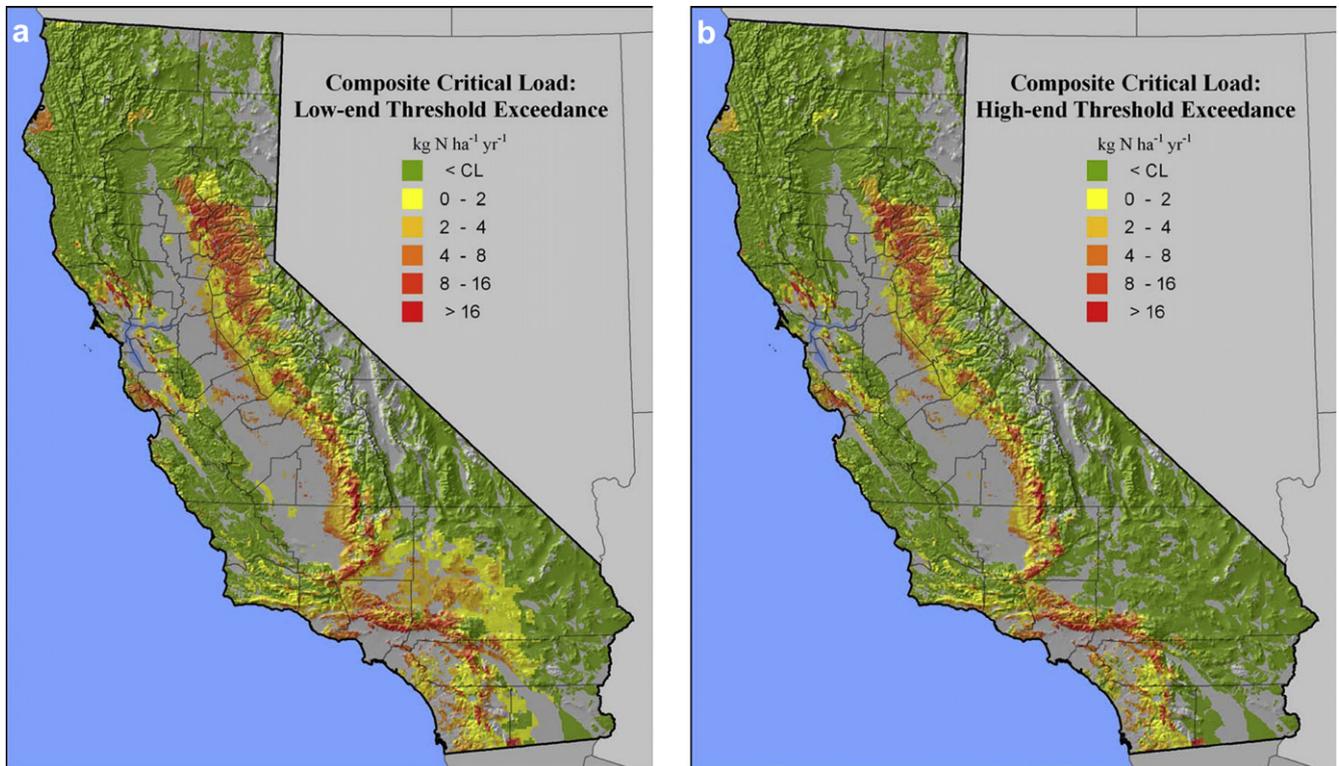


Fig. 12. Composite CL exceedance maps for all seven vegetation types included in this study showing the combined exceedance areas and the level of exceedance ($\text{kg N ha}^{-1} \text{yr}^{-1}$). When CLs based on two different N responders were used within a given vegetation type (e.g., lichen effects and nitrate leaching), only the more sensitive responder was used (lowest CL). (a) The lowest value of two CLs was used in the case of coastal sage scrub, mixed conifer forest (lichen community effects), desert scrub and pinyon-juniper, and the lichen effects CL was used for chaparral. (b) The higher CL values were used when more than two values were available for a given vegetation type.

declines, resulting in a lower tendency to leach NO_3^- . However, in some scenarios, vegetation may decrease resulting in lower evapotranspiration and greater runoff (Tague et al., 2009) and presumably lower CLs for NO_3^- leaching.

Climate change effects on the CLs for weedy invasives and associated accumulation of biomass sufficient to sustain fire spread in desert vegetation are expected to be similar to that described above for NO_3^- leaching. Enhanced N accumulation in dry years followed by irregularly occurring wet years or extreme precipitation events may stimulate biomass production as a result of increased availability of water and N. Of course, this scenario assumes that wet years are not characterized by extreme precipitation in which most of the moisture is rapidly lost as runoff with little effect on vegetative growth.

Lichen CL values are directly affected by precipitation amounts, with higher CLs with increasing precipitation (Geiser et al., 2010), presumably a result of leaching of N from lichen thalli. Thus, lichen communities may be more impacted by N in dry climates and less affected by N in wet climates or after large precipitation events. This also begs the question as to whether a larger fraction of precipitation falling as rain instead of snow will more effectively leach N from lichen tissue in montane areas and thus reduce N effects, resulting in a higher CL for effects on epiphytic lichens. Increasing nutrient availability allows mesotrophic and eutrophic species to tolerate colder climate zones (Table 6 in Geiser and Neitlich, 2007).

Other soil-mediated effects of excess N (e.g., changes in mycorrhizal communities, reduced fine root biomass production) are also expected to be similarly affected by the altered precipitation regime described above. However, we recognize that many complex interacting factors of ecological importance will be affected by future climate change and it is difficult to predict outcomes or which factors may ultimately be the most important in

affecting ecosystem sensitivity to N deposition. If climate change alters fire frequency and intensity in some vegetation types, this could affect CLs in various ways, such as by reducing site N capital, altering plant N demand and succession, sometimes resulting in plant type conversion.

3.10. Management options for N-impacted ecosystems

Gundersen et al. (2006) listed five ways that management options may alleviate N saturation in temperate forest ecosystems: (1) reducing N input, (2) increasing N uptake, (3) increasing N export in harvests, (4) restoring soil N retention, and (5) improving catchment-scale N removal (e.g., in the riparian zone). In ecosystems detrimentally affected by N deposition, silvicultural treatments can often be applied to improve site condition, but invariably reductions in N deposition are also needed for sustainable improvements (Gimeno et al., 2009; Gundersen et al., 2006; Rothe and Mellert, 2004).

Management options for mitigating the effects of excess N vary widely among vegetation types because of differing resource impacts caused by N deposition. For instance, invasive species are highly responsive to N and have caused declines in native species and increased fire frequency in deserts and CSS (Allen et al., 1998, 2009; Brooks et al., 2004), prompting a focus on invasive species management. At the opposite end of the productivity spectrum, forest stands have not experienced major species shifts. But physiological changes in trees, such as reduced root:shoot ratios that may affect tree response to drought and bark beetle attack, are a concern in highly N-polluted ecosystems. Likewise, elevated N pollution in streams is a concern in N-saturated chaparral and forested catchments. Economic and resource values of ecosystems also dictate the type of management for elevated N. Most California ecosystems harbor endangered species (Skinner and Pavlik, 1997)

and these are especially numerous in vegetation types with limited distributions such as serpentine grasslands and coastal sage scrub. Management to conserve endangered species threatened by N deposition focuses on invasive species control.

In many cases no management options can or will be implemented in ecosystems impacted by excess N. Treatment options may not be technically feasible or cost effective, and in many protected areas site manipulations are prohibited. Resources to carry out the treatments may not be available, and in many cases land managers aren't fully aware of the effects of N excess, or other management priorities and concerns take precedence. When prescribed fire seems an appropriate management tool, implementation of prescribed fire may be prohibited because of public opinion, issues with air quality impacts from fire emissions, risk of fire escape, or lack of resources to apply prescribed fire treatments. Frequently, management treatments for the effects of excess N will only be applied in local high-interest situations such as where threatened and endangered species habitat is impacted by N deposition or in areas heavily visited for recreation.

3.10.1. Management options for forests in exceedance of the critical load

Management options for mitigating the effects of excess N in mixed conifer forests are based on reducing N deposition inputs and treatments for reducing N pools in the ecosystem and to enhance plant and microbial N demand. Fire has a limited capacity to release N from the mineral soil where commonly 60–80% of ecosystem N capital is stored (Bauer et al., 2000; Kreutzer et al., 2009; Verburg and Johnson, 2001), with particularly high values in systems with low humus accumulation (Johnson et al., 2009). Volatilization losses of N during prescribed fires are believed to be lower in forests than in chaparral shrublands because of the lower temperatures in soil, litter and duff of forest fires (DeBano, 1982). Thus prescribed fire at repeated intervals, in combination with reduced N deposition is needed to eventually mitigate or reverse the symptoms of N excess. Simulated scenarios for highly-polluted mixed conifer forests in southern California indicate that the occurrence of prescribed fires every 15 years and 50–75% reductions in N deposition were the most effective treatments for N-saturated catchments. Nonetheless, even prescribed fire at longer intervals (30–60 years) and 25–50% decreases in N deposition still resulted in large decreases in ecosystem N, and could be considered as major progress in improving ecosystem condition (Gimeno et al., 2009).

The combined effects of ozone, N deposition and long-term fire suppression in southern California forests have resulted in large accumulations of C and N as necromass and woody fuels and in aboveground biomass. The latter effect is a result of the role of ozone and N enrichment in reducing C allocation belowground (Grulke et al., 2009). Thus, a larger fraction of the total ecosystem N may be allocated aboveground than in unpolluted forests, and particularly compared to unpolluted forests that also experience periodic burning. These factors support the usefulness of prescribed fire as a management option for mitigating N saturation conditions because a larger proportion of site N capital is aboveground where it can be burned, although excessive fuel and duff buildup can also make it difficult to implement an effective burn without causing excessive damage to roots or boles (Stephens and Finney, 2002). However, even in these polluted catchments we estimate that as much as 65–80% of site N capital may be stored belowground where fire is not effective at releasing the stored N (Johnson et al., 2009). In addition, prescribed fire can be difficult to implement in the urban–wildland interface that characterizes the most polluted forests in California.

Silvicultural options for increasing plant demand for N have not been tested, but could include such treatments as prescribed fire or

mechanical stand thinning to encourage vigorous regrowth of understory and overstory vegetation. However, the only viable option for protecting sensitive native epiphytic lichen communities would seem to be much greater reductions in N emissions and deposition over large areas of the state of California. Applying wood chips to the soil in harvested areas of a northern hardwood forest with elevated N deposition immobilized N and was effective in reducing NO_3^- leaching (Homyak et al., 2008). Similar approaches could be tried in N-saturated stands in California to enhance N retention following disturbances such as fire or harvesting, although such methods are labor intensive, and prescribed fire can be difficult to implement in the urban–wildland interface characterizing the most polluted forests in California.

3.10.2. Management options for chaparral and oak woodlands in exceedance of the critical load

Few options are available for reversing the high N losses from N-saturated chaparral catchments. Post-fire streamwater monitoring in N-saturated chaparral catchments in the San Dimas Experimental Forest over a 15-year monitoring period indicated that prescribed fire was not an effective option for reducing N losses in streamwater in severely N-saturated catchments exposed to elevated N deposition for approximately 50 years (Fenn et al., 2008; Meixner et al., 2006). As discussed for forest ecosystems, fire has limited capacity to reduce N pools in the mineral soil. In three different chaparral fire studies 7–10% of total ecosystem N was lost during burns (Rundel and Vankat, 1989). However, volatilization of soil N in chaparral fires is minor because mineral soils even at a depth of 2.5 cm don't reach temperatures high enough ($\geq 250^\circ\text{C}$; DeBano, 1982) to volatilize significant amounts of N even in severe burns (Christensen, 1994; DeBano, 1982). However, post-fire erosion losses of N can be significant (Christensen, 1994). In areas with extensive fuel accumulation, smoldering fires can heat the soil to a depth of 10–20 cm (Christensen, 1994), but N volatilization is still expected to be small compared to the total N stored in the soil profile. Following fire, the soil has a high potential to mineralize N, followed by high nitrification rates (Fenn et al., 1993; Riggan et al., 1994), favoring NO_3^- export losses.

The significance of the above-mentioned factors for management of N-saturated chaparral catchments is that decreases in N deposition are ultimately required to more fully mitigate the symptoms of excess N. Although prescribed fire alone isn't enough to reverse the symptoms of N saturation, fire does result in release of N from the system, suggesting that if N deposition inputs are reduced sufficiently, over time periodic fire should help return chaparral vegetation to a condition of conservative N cycling. However, the time required for this would depend on site history and environmental conditions, the amount of N accumulated in the system and current and future rates of N deposition. As concluded for lichen community effects in forests, reducing N deposition to levels below the lichen-based CL is the only mechanism for reducing the impacts of N deposition on lichen communities in chaparral and oak woodlands. Because of the high sensitivity of lichens to N deposition, in many areas of southern and central California a 3–9 fold reduction from current inputs may be required to allow improvements in lichen community conditions.

3.10.3. Management options for coastal sage scrub in exceedance of the critical load

The two major problems facing CSS under high N deposition are increased exotic grass production and loss of native species diversity. A number of approaches have been used to manage exotic grasses and increase native plants. California is well known for

a two-century history of vegetation-type conversion to exotic annual grassland (Minnich, 2008), but the conversion in CSS has occurred in the last 40–50 years (Allen et al., 1998; Minnich and Dezzani, 1998; Talluto and Suding, 2008). This poses a threat to the many rare species that are protected under the Endangered Species Act, and has resulted in a flurry of activity to restore CSS shrubs and understory forbs. Much of the effort is aimed at seed-bank control for exotic annuals. The seedbank of exotics in remnant CSS sites with relatively low N deposition ($8 \text{ kg ha}^{-1} \text{ yr}^{-1}$) was up to $10,000 \text{ seeds m}^{-2}$, while that of native species was only 600 seeds m^{-2} (Cox and Allen, 2008a). In a site with higher N deposition ($15 \text{ kg ha}^{-1} \text{ yr}^{-1}$ and perhaps historically higher), there was no native seedbank left at all, and the site was completely covered with exotic grasses and forbs (Cione et al., 2002).

The methods used for grass control in CSS include fire, herbicides, mowing, mulch to immobilize N, grazing, and solarization using plastic. The most effective large-scale method for controlling annual grasses is burning in the spring before seeds have shattered. This method is effective in perennial grasslands that resprout after fire (Gillespie and Allen, 2004), but fire has not been used in remnant CSS because managers are understandably reluctant to burn remnant stands of shrubs. Fire is, however, effective in CSS that has been type-converted to annual grassland, and is used in local preserves where permitted. The seedbank of exotics may be reduced by two orders of magnitude after fire, providing a window of opportunity to seed native species at a time when exotics are not so abundant (Cox and Allen, 2008a). Solarization, or soil heating using plastic, has been used effectively in small plots to control the weed seedbank in abandoned agricultural lands, and promoted greater establishment of native CSS species than mowing or herbicides (Marushia and Allen, 2010).

Mowing and other methods of mechanical control of exotics have proved effective where fire and other methods cannot be used for regulatory reasons. CSS has been reestablished using mechanical control plus seeding (DeSimone, 2007). Continuous annual mowing of exotic grasses in spring allowed gradual recolonization of native shrubs from a nearby seed source (Eliza Maher, Center for Natural Lands Management, pers. comm.). Grazing was effective for grass control in highly invaded CSS in a wet year when there was sufficient grass forage, but not in dry years. Furthermore, grazing would need to be applied at 5-year intervals as the grass recovers to pre-treatment cover within this time period (Allen et al., 2005). Grazing is more effective in grasslands with more reliable annual precipitation (Weiss, 1999; See Section 3.7.4).

Grass-specific herbicides are effective for controlling annual grasses (Cione et al., 2002; Allen et al., 2005; Cox and Allen, 2008b; Steers and Allen, 2010). However, exotic forbs increased more than native plants in most of these studies, and shrubs established poorly in spite of seeding. This indicates that shrubs are part of a competitive hierarchy in order of decreasing aggressiveness from exotic annual grasses, exotic forbs, native forbs, and native shrub seedlings (Cox and Allen, 2008b). Current research focuses on control of exotic forbs to enable greater establishment of native species.

Mulch to immobilize N has been used for restoration of N-impacted CSS (Zink and Allen, 1998; Cione et al., 2002). The impacts of added carbon on N immobilization are short-term (Corbin and D'Antonio, 2004), so native species must establish quickly to take advantage of reduced soil N and reduced competition with nitrophilous exotic grasses. A more impractical aspect of mulching is that it can only be used for relatively small-scale restorations, and not for a landscape impacted by N deposition. Fire, herbicides, grazing, or mowing to reduce exotic grass cover will be more useful for large-scale mitigation of N deposition impacts on grass productivity.

3.10.4. Management options for grassland in exceedance of the critical load

In the face of continued deposition above the CL, management of grasslands to maintain native biodiversity is essential. Exotic annual grasses will never be completely eliminated from such systems. The key management goal is to reduce annual grass cover and thatch/litter accumulation enough that the native forbs can coexist at sufficient densities to provide habitat for species such as the Bay checkerspot butterfly.

In the south San Francisco Bay, invasions of annual grasses are effectively controlled by moderate grazing (Fig. 4a; 1 cow–calf pair per 4 ha). Removing cattle in high deposition areas is disastrous for the native biodiversity of the grassland, as high grass biomass leads to litter accumulation that effectively smothers the grassland with 1+ cm of thatch. Cattle selectively eat the nutritious annual grasses, reduce biomass accumulation, and mechanically break down litter leaving sufficient bare mineral soil and open canopy for the short annual forbs. Both winter–spring (wet season) and summer–fall (dry season) grazing are effective (Weiss, 1999), and a mosaic of different grazing regimes is advantageous in spreading risks across different weather years. The exact timing of grazing is determined by experienced ranchers based on range condition and cattle weight gains.

In N deposition affected grasslands, selective herbivory on N-rich grasses is an essential process in maintaining local diversity. Moderate grazing (defined by appropriate intensity and timing) can result in healthy ecosystems with high native biodiversity (Weiss, 1999; Marty, 2005). By consuming large amounts of (primarily) grass forage, grazers cycle and redistribute nutrients (“eat globally, deposit locally”; Weiss, 1999), physically disturb the soil surface, provide open germination sites for many native species, and export some N as animal biomass. But, the negative effects of overgrazing, including degraded riparian zones, soil compaction, increased erosion, and the spread of weeds, have been apparent over many poorly managed rangelands (Jackson and Bartolome, 2007).

At Edgewood, on the coastal San Francisco peninsula where the grassland CL was determined along a roadside gradient, the degraded areas are too small (~10 ha) for effective grazing. A rotational mowing regime has been implemented. In early May, when the *Lolium* seeds have not fully ripened but most annual herbs have set seed, mechanical mowing with a low cut (5 cm) takes off *Lolium* seed heads and little or no regrowth is observed. Later in the dry season (September) the thatch is broken up (if needed) with a harrow rake. Mowing has obvious positive effects (Fig. 4b), reducing grass cover and increasing native forb cover, including a three-fold increase in *Plantago* cover. The positive effects of mowing last for 3–5 years until regrowth of *Lolium* and thatch accumulation necessitate another mowing.

Prescribed fire can also reduce annual grass and thatch cover. Late-spring burns (May–June) are most effective because grass seeds have not dropped and are vulnerable to fire. Spring burns have been followed by a flush of high forb cover when sufficient seedbank was present, but habitats that have been overgrown by grasses for >3–4 years have lost much of the forb seedbank and do not show as strong of a post-fire increase in forb cover. Summer and fall burns have not been effective, except for reducing thatch cover, because grass seeds on the ground can survive and the post-fire germination and growth conditions are highly suitable for rapid grass growth. The positive effects of fire last only 2–3 years, so late-spring burns are considered an initial treatment for restoration and must be followed by grazing to control grass regrowth. Logistical and institutional barriers currently prohibit widespread use of prescribed fire in this ecosystem.

Because the Bay checkerspot butterfly is protected under the US Endangered Species Act as a Threatened Species, novel mitigation

for new emissions sources in the South Bay has been implemented since 2001. The first mitigation project was the Metcalf Energy Center, a 600 MW natural gas-fired power plant. Agreements between the US Fish and Wildlife Service, California Energy Commission, and Calpine Corporation set a local precedent for addressing N deposition impacts. As of 2008, mitigation for new natural gas-fired power plants and road expansion includes permanent protection of >300 ha of prime serpentine grassland, along with endowments for monitoring and adaptive management that now exceed \$2.5 million (Mayall, 2008). Acquisition includes fee-title and conservation easements on each mitigation property held by different entities. Monitoring includes surveys of Bay checkerspot butterfly populations, permanent transects measuring detailed composition of the grassland, rare plant surveys, weed control, and other activities that are presented in annual reports. On-going consultations with ranchers lead to fine-tuning of the grazing management.

Because the N deposition issue is regional in scale, the result of many point, line, and area sources that create a large pollution plume, a larger mitigation effort that avoids the pitfalls of project by project mitigation is underway. The remaining 1500+ ha of serpentine grassland on Coyote Ridge are being targeted by the Santa Clara County Habitat Conservation Plan/Natural Communities Conservation Plan, with N deposition impacts as one nexus for action. (www.scv-habitatplan.org). This habitat conservation plan will include rigorous standards for acquisition, monitoring, and adaptive management, using the initial mitigation projects as models.

3.10.5. Management options for desert in exceedance of the critical load

The problem of invasive annuals and frequent fire has only recently received attention in the desert, and restoration research has just begun on this problem. Past research and practice in the hot deserts have emphasized restoring disturbances such as pipelines and recreational vehicle tracks (Bainbridge, 2007). Methods of propagating and planting desert shrubs have been the focus, especially methods such as deep irrigation to assure survival of transplants. Hand control of invasive grasses and forbs is recommended where shrub seedlings are to be established, but relatively little large-scale control of exotic annuals has been done. The Weed Management Areas (http://www.cdca.ca.gov/phpps/ipc/weedmgtaareas/wma_index_hp.htm) have been designated in deserts (as well as other ecoregions) to help control invasive species, and N-responsive grasses such as *Bromus rubens* are considered high-priority for control in order to reduce fire frequency and competition with native flowers. To determine the biodiversity impacts of invasive species, removal studies have been done on *Brassica tournefortii* (Barrows et al., 2009), *S. barbatus* and *B. rubens* (Steers and Allen, 2010). These studies show losses in native plant and animal abundance and richness under exotic invasions, and recommend methods for control such as grass-specific herbicides and mowing. However, controlling invasive grasses over large expanses of N-eutrophied desert will be expensive, and the ultimate solution to preserve diversity and reduce fire frequency will be to reduce air pollution.

4. Conclusions

The ideal management option for reducing effects of N excess is improved air quality. Although NO_x emissions are declining in California (Cox et al., 2009), NH_x emissions are not decreasing to a similar extent if at all and N deposition in California is expected to remain high for the foreseeable future, thus pointing to the need for additional management options. However, improvement or protection of epiphytic lichen communities from the effects of

atmospheric N can only be achieved by reducing their exposure to N pollution. In low biomass ecosystems such as CSS, desert or grasslands that are plagued by invasive annual grasses, removal or control of grasses or grass seeding can be achieved by treatments such as mowing, grazing, manual weeding, the use of grass-selective herbicides or burning. However, such treatments require periodic application to be effective, and may be limited in practice due to local concerns or restrictions related to protected lands, the use of fire or herbicides, or because methods are labor intensive.

In woody biomass dominated systems such as chaparral, woodlands or forests, management strategies focus on reduction of accumulated N as a result of chronic atmospheric inputs. Even with reductions in N deposition, if N has accumulated in the plant/soil system, management practices to reduce N stores will be needed to facilitate the return to more typical N accumulation and conservative N cycling. Possible methods for removing excess N include prescribed fire, thinning and various harvest techniques. The major problem with these methods is their limited capacity to liberate N stored in the mineral soil, where 65–80% of site N capital is stored in forest ecosystems in California (Johnson et al., 2009), compared to 80–95% in soils of California chaparral (Rundel and Parsons, 1980; Rundel and Vankat, 1989). A meta-analysis of fire effects on N pools in terrestrial ecosystems showed that the mean change in total soil N after fire was only 3% (Wan et al., 2001). The effectiveness of vegetation management treatments in reversing the effects of N deposition will depend partly on the size of the accumulated N pools, the on-going rate of N deposition, and the potential for treatments to enhance the release or removal of stored N.

We estimate that one-third of the land area of the seven major California vegetation types considered is in excess of the N CL. This result highlights the major ecological and environmental significance of N deposition in California. A key factor leading to such an extensive area in exceedance is the high N sensitivity of epiphytic lichen communities and plant communities within low biomass and N poor ecosystems. For example, coastal sage scrub and grasslands ecosystems have low CL values of 6–8 kg ha⁻¹ yr⁻¹, and are at low elevation close to emissions sources, with 54 and 44% of these areas in exceedance of the CL. Similarly, 40–50% of the oak woodland and chaparral areas are in exceedance of the lichen-based CL. In contrast only about 5% of forest and 3–15% of chaparral coverage is in exceedance of the NO₃⁻ leaching CL, yet this encompasses an estimated six to eight thousand km² of land area. For grasslands, desert and CSS N deposition in exceedance of the CL represents risk of vegetation-type conversion, clearly a dramatic and undesirable effect. In the most polluted forests (e.g., estimated N deposition ≥ 25–35 kg ha⁻¹ yr⁻¹) N deposition in conjunction with ozone threatens forest sustainability by contributing to multiple stress complexes, thus increasing forest mortality and fire risk (Grulke et al., 2009). However, the N CL for this effect is not well defined. In summary, this overview of the spatial extent and specific ecological effects of N deposition in California ecosystems highlights the difficulty in mitigating N excess effects by way of vegetation management options alone and the need for much greater reductions in N emissions in California.

Acknowledgements

The US Forest Service-Pacific Northwest Research Station of the Forest Inventory and Analysis Program, and US Forest Service-Pacific Northwest Region Air Resource Management Program provided funding for data analysis of and access to lichen data. This research was funded in part by a National Science Foundation grant (NSF DEB 04-21530).

References

- Aber, J.D., Goodale, C.L., Ollinger, S.V., Smith, M.L., Magill, A.H., Martin, M.E., Hallett, R.A., Stoddard, J.L., 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? *BioScience* 53, 375–389.
- Allen, E.B., Temple, P.J., Bytnerowicz, A., Arbaugh, M.J., Sirulnik, A.G., Rao, L.E., 2007. Patterns of understory diversity in mixed coniferous forests of southern California impacted by air pollution. *The Scientific World Journal* 7 (S1), 247–263. doi:10.1100/tsw.2007.72.
- Allen, E.B., Cox, R.D., Tennant, T., Kee, S.N., Deutschman, D.H., 2005. Landscape restoration in southern California forblands: response of abandoned farmland to invasive annual grass control. *Israel Journal of Plant Sciences* 53, 237–245.
- Allen, E.B., Padgett, P.E., Bytnerowicz, A., Minnich, R., 1998. Nitrogen deposition effects on coastal sage vegetation of southern California. Proceedings of the International Symposium on Air Pollution and Climate Change Effects on Forest Ecosystems, Riverside, California, February 5–9, 1996. USDA Forest Service, Pacific Southwest Research Station. PSW-GTR-166, pp. 131–140. Available from: <http://www.fs.fed.us/psw/publications/gtrs.shtml>.
- Allen, E.B., Rao, L.E., Steers, R.J., Bytnerowicz, A., Fenn, M.E., 2009. Impacts of atmospheric nitrogen deposition on vegetation and soils in Joshua Tree National Park. In: Webb, R.H., Fenstermaker, L.F., Heaton, J.S., Hughson, D.L., McDonald, E.V., Miller, D.M. (Eds.), *The Mojave Desert: Ecosystem Processes and Sustainability*. University of Nevada Press, Las Vegas, pp. 78–100.
- Ávila, A., Rodrigo, A., Rodá, F., 2002. Nitrogen circulation in a Mediterranean holm oak forest, La Castanya, Montseny, northeastern Spain. *Hydrology and Earth System Science* 6, 551–557.
- Baez, S., Fargione, J., Moore, D.I., Collins, S.L., Gosz, J.R., 2007. Atmospheric nitrogen deposition in the northern Chihuahuan desert: temporal trends and potential consequences. *Journal of Arid Environments* 68, 640–651.
- Bainbridge, D.A., 2007. *A Guide for Desert and Dryland Restoration*. New Hope for Arid Lands. Island Press, Washington, D.C.
- Barrows, C.W., Allen, E.B., Brooks, M.L., Allen, M.L., 2009. Effects of an invasive plant on a desert sand dune landscape. *Biological Invasions* 11, 673–686.
- Battye, W., Aneja, V.P., Roelle, P.A., 2003. Evaluation and improvement of ammonia emissions inventories. *Atmospheric Environment* 37, 3873–3883.
- Bauer, G.A., Persson, H., Persson, T., Mund, M., Hein, M., Kummert, E., Matteucci, G., van Oene, H., Scarascia-Mugnozza, G., Schulze, E.-D., 2000. Linking plant nutrition and ecosystem processes. In: Schulze, E.-D. (Ed.), *Carbon and Nitrogen Cycling in European Forest Ecosystems*. Ecological Studies, vol. 142. Springer-Verlag, Berlin, pp. 63–98.
- Baum, M.M., Kiyomiya, E.S., Kumar, S., Lappas, A.M., Kapinus, V.A., Lord III, H.C., 2001. Multicomponent remote sensing of vehicle exhaust by dispersive absorption spectroscopy. 2. Direct on-road ammonia measurements. *Environmental Science & Technology* 35, 3735–3741.
- Bishop, G.A., Peddle, A.M., Stedman, D.H., 2010. On-road emission measurements of reactive nitrogen compounds from three California cities. *Environmental Science & Technology* 44, 3616–3620.
- Blanchard, C.L., Michaels, H., Tannenbaum, S., 1996. Regional Estimates of Acid Deposition Fluxes in California for 1985–1994. Final Report for Contract No. 93-332. California Air Resources Board, Sacramento.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinnerby, S., Davidson, E., Dentener, F., Emmett, B., Erismann, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., de Vries, W., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecological Applications* 20, 30–59.
- Bobbink, R., Ashmore, M.R., Braun, S., Fluckiger, W., van der Wyngaert, I.J.J., 2003. Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update. In: Achermann, B., Bobbink, R. (Eds.), *Empirical Critical Loads for Nitrogen*, Environmental Documentation 164, Background document for Expert Workshop on Empirical Critical Loads for Nitrogen on Semi-natural Ecosystems, 11–13 November 2002. Swiss Agency for the Environment, Forests and Landscape, Berne, Switzerland, pp. 43–170. Available from: <http://www.iap.ch/publikationen/nworkshop-background.pdf>.
- Bobbink, R., Roelofs, J.G.M., 1995. Critical loads for natural and semi-natural ecosystems: the empirical approach. *Water, Air, and Soil Pollution* 85, 2413–2418.
- Bowman, W.D., Gartner, J.R., Holland, K., Wiedermann, M., 2006. Nitrogen critical loads for alpine vegetation and terrestrial ecosystem response: are we there yet? *Ecological Applications* 16, 1183–1193.
- Breiner, J., Gimeno, B.S., Fenn, M., 2007. Calculation of theoretical and empirical nutrient N critical loads in the mixed-conifer ecosystems of southern California. *The Scientific World Journal* 7 (S1), 198–205. doi:10.1100/tsw.2007.65.
- Bromirski, P.D., Flick, R.E., 2008. Storm surge in the San Francisco Bay/Delta and nearby coastal locations. *Shore and Beach* 76, 29–37.
- Brooks, M.L., 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* 40, 344–353.
- Brooks, M.L., Minnich, R.A., 2006. Southeastern deserts bioregion. In: Sugihara, N.G., Wagtendonk, J.W.V., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), *Fire in California's Ecosystems*. University of California Press, Berkeley, pp. 391–414.
- Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M., Pyke, D., 2004. Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688.
- Brooks, M.L., Matchett, J.R., 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *Journal of Arid Environments* 67, 148–164.
- Bytnerowicz, A., Arbaugh, A., Schilling, S., Fraczek, W., Alexander, D., Dawson, P., 2007. Air pollution distribution patterns in the San Bernardino Mountains of southern California: a 40-year perspective. *The Scientific World Journal* 7 (S1), 98–109. doi:10.1100/tsw.2007.57.
- Bytnerowicz, A., Sanz, M.J., Arbaugh, M.J., Padgett, P.E., Jones, D.P., Davila, A., 2005. Passive sampler for monitoring ambient nitric acid (HNO₃) and nitrous acid (HNO₂) concentrations. *Atmospheric Environment* 39, 2655–2660.
- Byun, D., Schere, K.L., 2006. Review of the governing equations, computational algorithms, and other components of the models-3 community multiscale air quality (CMAQ) modeling system. *Applied Mechanics Reviews* 59, 51–77.
- Cayan, D.R., Maurer, E.P., Dettinger, M.D., Tyree, M., Hayhoe, K., 2008. Climate change scenarios for the California region. *Climatic Change* 87 (Suppl. 1), S21–S42.
- CCSP, 2008. *Weather and Climate Extremes in a Changing Climate. Regions of Focus: North America, Hawaii, Caribbean, and U.S. Pacific Islands*. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. Karl, T.R., et al. (Eds.), Department of Commerce, NOAA's National Climatic Data Center, Washington, D.C., USA, 164 pp.
- Choi, Y.D., Temperton, V.M., Allen, E.B., Grootjans, A.P., Halassy, M., Hobbs, R.J., Naeth, M.A., Torok, K., 2008. Ecological restoration for future sustainability in a changing environment. *Ecoscience* 15, 53–64.
- Christensen, N.L., 1994. The effects of fire on physical and chemical properties of soil in Mediterranean-climate shrublands. In: Moreno, J.M., Oechel, W.C. (Eds.), *The Role of Fire in Mediterranean-Type Ecosystems*. Ecological Studies, vol. 107. Springer-Verlag, New York, pp. 79–95.
- Cione, N.K., Padgett, P.E., Allen, E.B., 2002. Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. *Restoration Ecology* 10, 376–384.
- Clarisse, L., Clerbaux, C., Dentener, F., Hurtmans, D., Coheur, P.-F., 2009. Global ammonia distribution derived from infrared satellite observations. *Nature Geoscience* 2, 479–483.
- Clark, C., in press. Great plains. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T. (Eds.), *Assessment of N deposition effects and empirical critical loads of N for ecoregions of the United States*. General Technical Report, USDA Forest Service, Northern Research Station, Newtown Square, PA (Chapter 11).
- Clark, C.M., Tilman, D., 2008. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature* 451, 712–715.
- Corbin, J.D., D'Antonio, C.M., 2004. Can carbon addition increase competitiveness of native grasses? A case study from California. *Restoration Ecology* 12, 36–43.
- Cox, P., Delao, A., Komorniczak, A., Weller, R., 2009. *The California Almanac of Emissions and Air Quality*, 2009 Edition. California Environmental Protection Agency, Air Resources Board, Sacramento, California.
- Cox, R.D., Allen, E.B., 2008a. Composition of soil seed banks in southern California coastal sage scrub and adjacent exotic grassland. *Plant Ecology* 198, 37–46.
- Cox, R.D., Allen, E.B., 2008b. Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. *Journal of Applied Ecology* 45, 495–504.
- Cresser, M.S., 2000. The critical loads concept: milestone or millstone for the new millennium? *The Science of the Total Environment* 249, 51–62.
- Davis, F.W., Stoms, D.M., Hollander, A.D., Thomas, K.A., Stine, P.A., Odion, D., Borchert, M.I., Thorne, J.H., Gray, M.V., Walker, R.E., Warner, K., Graae, J., 1998. *The California Gap Analysis Project—Final Report*. University of California, Santa Barbara, CA. Available from: http://www.biogeog.ucsb.edu/projects/gap/gap_rep.html (accessed 29.10.09).
- DeBano, L.F., 1982. Assessing the effects of management actions on soils and mineral cycling in Mediterranean ecosystems. In: Conrad, C.E., Oechel, W.C. (Tech. Coordinators), *Proceedings of the Symposium on Dynamics and Management of Mediterranean-Type Ecosystems*. Gen. Tech. Rep. PSW-58. Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Berkeley, California, pp. 345–350.
- DeSimone, S.A., 2007. Non-chemical restoration of coastal sage scrub in artichoke-infested grasslands (California). *Ecological Restoration* 24, 278–279.
- De Vries, W., Kros, H., Reinds, G.J., Wamelink, W., Mol, J., van Dobben, H., Bobbink, R., Emmett, B., Smart, S., Evans, C., Schlutow, A., Kraft, P., Belyazid, S., Sverdrup, H., van Hinsberg, A., Posch, M., Hettelingh, J.-P., 2007. *Developments in Deriving Critical Limits and Modeling Critical Loads of Nitrogen for Terrestrial Ecosystems in Europe*. Alterra, Alterra-Rapport 1382. Wageningen, The Netherlands, 206 pp.
- Durbin, T.D., Wilson, R.D., Norbeck, J.M., Miller, J.W., Huai, T., Rhee, S.H., 2002. Estimates of the emission rates of ammonia from light-duty vehicles using standard chassis dynamometer test cycles. *Atmospheric Environment* 36, 1475–1482.
- Egerton-Warburton, L.M., Allen, E.B., 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications* 10, 484–496.
- Egerton-Warburton, L.M., Johnson, N.C., Allen, E.B., 2007. Mycorrhizal community dynamics following nitrogen fertilization: a cross-site test in five grasslands. *Ecological Monographs* 77, 527–544.
- Ehrlich, P.R., Haanski, I. (Eds.), 2004. *On the Wings of Checkerspot: A Model system for Population Biology*. Oxford University Press, New York.
- Fenn, M.E., Poth, M.A., 2004. Monitoring nitrogen deposition in throughfall using ion exchange resin columns: a field test in the San Bernardino Mountains. *Journal of Environmental Quality* 33, 2007–2014.

- Fenn, M.E., Poth, M.A., 1999. Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, southern California. *Journal of Environmental Quality* 28, 822–836.
- Fenn, M.E., Poth, M.A., Aber, J.D., Baron, J.S., Bormann, B.T., Johnson, D.W., Lemly, A.D., McNulty, S.G., Ryan, D.F., Stottlemeyer, R., 1998. Nitrogen excess in North American ecosystems: predisposing factors, ecosystem responses, and management strategies. *Ecological Applications* 8, 706–733.
- Fenn, M.E., Sickman, J.O., Bytnerowicz, A., Clow, D.W., Molotch, N.P., Pleim, J.E., Tonnesen, G.S., Weathers, K.C., Padgett, P.E., Campbell, D.H., 2009. Methods for measuring atmospheric nitrogen deposition inputs in arid and montane ecosystems of western North America. In: Legge, A.H. (Ed.), *Air Quality and Ecological Impacts: Relating Sources to Effects*. Developments in Environmental Science, vol. 9. Elsevier, Amsterdam, pp. 179–228.
- Fenn, M.E., Haeuber, R., Tonnesen, G.S., Baron, J.S., Grossman-Clarke, S., Hope, D., Jaffe, D.A., Copeland, S., Geiser, L., Rueth, H.M., Sickman, J.O., 2003a. Nitrogen emissions, deposition, and monitoring in the western United States. *Bioscience* 53, 391–403.
- Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T., Johnson, D.W., Neitlich, P., 2003b. Ecological effects of nitrogen deposition in the western United States. *Bioscience* 53, 404–420.
- Fenn, M.E., Poth, M.A., Bytnerowicz, A., Sickman, J.O., Takemoto, B.K., 2003c. Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada. In: Bytnerowicz, A., Arbaugh, M.J., Alonso, R. (Eds.), *Ozone Air Pollution in the Sierra Nevada: Distribution and Effects on Forests*. Developments in Environmental Science, vol. 2. Elsevier, Amsterdam, pp. 111–155.
- Fenn, M.E., Geiser, L., Bachman, R., Blubaugh, T.J., Bytnerowicz, A., 2007. Atmospheric deposition inputs and effects on lichen chemistry and indicator species in the Columbia River Gorge, USA. *Environmental Pollution* 146, 77–91.
- Fenn, M.E., Jovan, S., Yuan, F., Geiser, L., Meixner, T., Gimeno, B.S., 2008. Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests. *Environmental Pollution* 155, 492–511.
- Fenn, M.E., Poth, M.A., Dunn, P.H., Barro, S.C., 1993. Microbial N and biomass, respiration and N-mineralization in soils beneath two chaparral species along a fire-induced age gradient. *Soil Biology and Biochemistry* 25, 457–466.
- Fenn, M.E., Poth, M.A., Johnson, D.W., 1996. Evidence for nitrogen saturation in the San Bernardino Mountains in southern California. *Forest Ecology and Management* 82, 211–230.
- Fenn, M.E., Allen, E.B., Geiser, L.H., Mediterranean California, in press. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T. (Eds.), *Assessment of N deposition effects and empirical critical loads of N for ecoregions of the United States*. General Technical Report, USDA Forest Service, Northern Research Station, Newtown Square, PA (Chapter 13).
- Fraser, M.P., Cass, G.R., 1998. Detection of excess ammonia emissions from in-use vehicles and the implications for fine particle control. *Environmental Science and Technology* 32, 1053–1057.
- Geiser, L.H., Jovan, S.E., Glavich, D.A., Porter, M.K., 2010. Lichen-based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington forests, USA. *Environmental Pollution* 158, 2412–2421.
- Geiser, L.H., Neitlich, P.N., 2007. Pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens. *Environmental Pollution* 145, 203–218.
- Gillespie, I.G., Allen, E.B., 2004. Fire and competition in a southern California grassland: impacts on the rare forb *Erodium macrophyllum*. *Journal of Applied Ecology* 41, 643–652.
- Gimeno, B.S., Yuan, F., Fenn, M.E., Meixner, T., 2009. Management options for mitigating nitrogen (N) losses from N saturated mixed conifer forests in California. In: Bytnerowicz, A., Arbaugh, M.J., Riebau, A.R., Andersen, C. (Eds.), *Wildland Fires and Air Pollution*. Developments in Environmental Science, vol. 8. Elsevier, Amsterdam, pp. 425–455.
- Grulke, N.E., Minnich, R.A., Paine, T.D., Seybold, S.J., Chavez, D.J., Fenn, M.E., Riggan, P.J., Dunn, A., 2009. Air pollution increases forest susceptibility to wildfires: a case study in the San Bernardino Mountains in southern California. In: Bytnerowicz, A., Arbaugh, M.J., Riebau, A.R., Andersen, C. (Eds.), *Wildland Fires and Air Pollution*. Developments in Environmental Science, vol. 8. Elsevier, Amsterdam, pp. 365–403.
- Grulke, N.E., Andersen, C.P., Fenn, M.E., Miller, P.R., 1998. Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California. *Environmental Pollution* 103, 63–73.
- Gundersen, P., Schmidt, I.K., Raulund-Rasmussen, K., 2006. Leaching of nitrate from temperate forests - effects of air pollution and forest management. *Environmental Reviews* 14, 1–57.
- Harpole, W.S., Goldstein, L., Aicher, R.J., 2007. Resource limitation. In: Stromberg, M.R., Corbin, J.D., D'Antonio, C.M. (Eds.), *California Grasslands: Ecology and Management*. University of California Press, Berkeley, pp. 119–127.
- Harrison, S.P., Viers, J.H., 2007. Serpentine grasslands. In: Stromberg, M.R., Corbin, J.D., D'Antonio, C.M. (Eds.), *California Grasslands: Ecology and Management*. University of California Press, Berkeley, pp. 145–155.
- Heywood, E., Hall, J., Reynolds, B., 2006. A review of uncertainties in the inputs to critical loads of acidity and nutrient nitrogen for woodland habitats. *Environmental Science & Policy* 9, 78–88.
- Hobbs, R., Mooney, H.A., 1995. Spatial and temporal variability in California annula grassland: results from a long-term study. *Journal of Vegetation Science* 6, 43–56.
- Homyak, P.M., Yanai, R.D., Burns, D.A., Briggs, R.D., Germain, R.H., 2008. Nitrogen immobilization by wood-chip application: protecting water quality in a northern hardwood forest. *Forest Ecology and Management* 255, 2589–2601.
- Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A., Vitousek, P.M., 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71, 478–491.
- Hull, J.C., Mooney, H.A., 1990. Effects of nitrogen on photosynthesis and growth of four California annual grasses. *Acta Oecologia* 11, 453–468.
- Hunsaker, C., Bytnerowicz, A., Auman, J., Cisneros, R., 2007. Air pollution and watershed research in the central Sierra Nevada of California: nitrogen and ozone. *The Scientific World Journal* 7 (S1), 98–109. doi:10.1100/tsw.2007.82.
- Inouye, R.S., 2006. Effects of shrub removal and nitrogen addition on soil moisture in sagebrush steppe. *Journal of Arid Environments* 65, 604–618.
- Jackson, R.D., Bartolome, J.W., 2007. Grazing ecology of California grasslands. In: Stromberg, M.R., Corbin, J.D., D'Antonio, C.M. (Eds.), *California Grasslands: Ecology and Management*. University of California Press, Berkeley, pp. 197–206.
- Johnson, D.W., Fenn, M.E., Miller, W.W., Hunsaker, C.F., 2009. Fire effects on carbon and nitrogen cycling in forests of the Sierra Nevada. In: Bytnerowicz, A., Arbaugh, M.J., Riebau, A.R., Andersen, C. (Eds.), *Wildland Fires and Air Pollution*. Developments in Environmental Science, vol. 8. Elsevier, Amsterdam, pp. 405–423.
- Jones, M.E., Paine, T.D., Fenn, M.E., Poth, M.A., 2004. Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions. *Forest Ecology and Management* 200, 67–76.
- Jovan, S., 2008. Lichen bioindication of biodiversity, air quality, and climate: Baseline results from monitoring in Washington, Oregon, and California. Gen. Tech. Rep. PNW-GTR-737. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 115 pp.
- Jovan, S., McCune, B., 2005. Air-quality bioindication in the greater central valley of California, with epiphytic macrolichen communities. *Ecological Applications* 15, 1712–1726.
- Kean, A.J., Harley, R.A., Littlejohn, D., Kendall, G.R., 2000. On-road measurement of ammonia and other motor vehicle exhaust emissions. *Environmental Science & Technology* 34, 3535–3539.
- Kreutzer, K., Butterbach-Bahl, K., Rennenberg, H., Papen, H., 2009. The complete nitrogen cycle of an N-saturated spruce forest ecosystem. *Plant Biology* 11, 643–649.
- Maron, J.L., Jefferies, R.L., 1999. Bush lupine mortality, altered resource availability, and alternative vegetation states. *Ecology* 80, 443–454.
- Marty, J.T., 2005. Effects of cattle grazing on diversity in ephemeral wetlands. *Conservation Biology* 19, 1626–1632.
- Marushia, R.G., Allen, E.B., 2010. Control of exotic annuals to restore native forbs in abandoned agricultural lands. *Restoration Ecology*. doi:10.1111/j.1526-100X.2009.00540.x.
- Mayall, D., 2008. Protecting coyote ridge. *Fremontia* 36, 12–19.
- Mayer, K.E., Laudenslayer, W.F., Jr., 1988. *A Guide to Wildlife Habitats of California*. State of California, Resources Agency, Department of Fish and Game, Sacramento. 166 pp. Available from: http://www.dfg.ca.gov/biogeodata/cwhr/wildlife_habitats.asp (accessed 29.10.09).
- Meixner, T., Fenn, M.E., Wohlgemuth, P., Oxford, M., Riggan, P., 2006. N saturation symptoms in chaparral catchments are not reversed by prescribed fire. *Environmental Science & Technology* 40, 2887–2894.
- Meixner, T., Fenn, M., 2004. Biogeochemical budgets in a Mediterranean catchment with high rates of atmospheric N deposition—importance of scale and temporal asynchrony. *Biogeochemistry* 70, 331–356.
- Michalski, G., Meixner, T., Fenn, M., Hernandez, L., Sirulnik, A., Allen, E., Thiemens, M., 2004. Tracing atmospheric nitrate deposition in a complex semi-arid ecosystem using $\Delta^{17}\text{O}$. *Environmental Science & Technology* 38, 2175–2181.
- Miller, N.L., Bashford, K.E., Strem, E., 2003. Potential impacts of climate change on California hydrology. *Journal of the American Water Resources Association* 39, 771–784.
- Minnich, R.A., Dezzani, R.J., 1998. Historical decline of coastal sage scrub in the Riverside-Perris plain, California. *Western Birds* 29, 366–391.
- Minnich, R.E., 2008. *California's Fading Flowers: Lost Legacy and Biological Invasions*. University of California Press, Berkeley.
- Nash III, T.H., Sigal, L.L., 1999. Epiphytic lichens in the San Bernardino Mountains in relation to oxidant gradients. In: Miller, P.R., McBride, J.R. (Eds.), *Oxidant Air Pollution in the Montane Forests of Southern California. A Case Study of the San Bernardino Mountains*. Ecological Studies, vol. 134. Springer, New York, pp. 223–234.
- Nordin, A., Strengbom, J., Witzell, J., Nasholm, T., Ericson, L., 2005. Nitrogen deposition and the biodiversity of boreal forests: Implications for the nitrogen critical load. *Ambio* 34, 20–24.
- Ogawa & Company, USA, Inc., 1998. NO, NO₂, NO_x and SO₂ sampling protocol using the Ogawa sampler. Users' Guide, version 4.0, February, 1998. Ogawa & Company, Pompano Beach, Florida.
- Padgett, P.E., Allen, E.B., Bytnerowicz, A., Minnich, R.A., 1999. Changes in soil inorganic nitrogen as related to atmospheric nitrogenous pollutants in southern California. *Atmospheric Environment* 33, 769–781.
- Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T. (Eds.), in press. *Assessment of N deposition effects and empirical critical loads of N for ecoregions of the United States*. General Technical Report, USDA Forest Service, Northern Research Station, Newtown Square, PA.
- Rao, L.E., Parker, D.R., Bytnerowicz, A., Allen, E.B., 2009. Nitrogen mineralization across an atmospheric nitrogen deposition gradient in southern California deserts. *Journal of Arid Environments* 73, 920–930.

- Rao, L.E., Allen, E.B., 2010. Combined effects of precipitation and nitrogen availability on native and invasive winter annual production in California deserts. *Oecologia* 162, 1035–1046.
- Rao, L.E., Allen, E.B., Meixner, T., 2010. Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts. *Ecological Applications* 20, 1320–1335.
- Reynolds, B., Wilson, E.J., Emmett, B.A., 1998. Evaluating critical loads of nutrient nitrogen and acidity for terrestrial systems using ecosystem-scale experiments (NITREX). *Forest Ecology and Management* 101, 81–94.
- Riggan, P.J., Lockwood, R.N., Lopez, E.N., 1985. Deposition and processing of airborne nitrogen pollutants in Mediterranean-type ecosystems of southern California. *Environmental Science & Technology* 19, 781–789.
- Riggan, P.J., Lockwood, R.N., Jacks, P.M., Colver, C.G., Weirich, F., DeBano, L.F., Brass, J.A., 1994. Effects of fire severity on nitrate mobilization in watersheds subject to chronic atmospheric deposition. *Environmental Science & Technology* 28, 369–375.
- Roadman, M.J., Scudlark, J.R., Meisinger, J.J., Ullman, W.J., 2003. Validation of Ogawa passive samplers for the determinations of gaseous ammonia concentrations in agricultural settings. *Atmospheric Environment* 37, 2317–2325.
- Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F.S., et al., 2009. A safe operating space for humanity. *Nature* 461, 472–475.
- Rodà, F., Ávila, A., Rodrigo, A., 2002. Nitrogen deposition in Mediterranean forests. *Environmental Pollution* 118, 205–213.
- Rodriguez-Lado, L., Montanarella, L., Macias, F., 2007. Evaluation of the sensitivity of European soils to the deposition of acid compounds: different approaches provide different results. *Water, Air, and Soil Pollution* 185, 293–303.
- Rothe, A., Mellert, K.H., 2004. Effects of forest management on nitrate concentrations in seepage water of forests in southern Bavaria, Germany. *Water, Air, and Soil Pollution* 156, 337–355.
- Rowlands, P.G., 1995. Regional bioclimatology of the California Desert. In: Latting, J., Rowlands, P.G. (Eds.), *The California Desert: An Introduction to Natural Resources and Man's Impact*. June Latting Books, Riverside, California, pp. 95–134.
- Rundel, P.W., Parsons, D.J., 1980. Nutrient changes in two chaparral shrubs along a fire-induced age gradient. *American Journal of Botany* 67, 51–58.
- Rundel, P.W., Vankat, J.L., 1989. Chaparral communities and ecosystems. In: Keeley, S.C. (Ed.), *The California Chaparral: Paradigms Reexamined*, No. 34, Science Series, Natural History Museum of Los Angeles County, Los Angeles, pp. 127–139.
- Scifres, C.J., Hamilton, W.T., 1993. *Prescribed Burning for Brushland Management: The South Texas Example*. Texas A & M University Press, College Station.
- Sigüenza, C., Corkidi, L., Allen, E.B., 2006a. Feedbacks of soil inoculum of mycorrhizal fungi altered by N deposition on the growth of a native shrub and an invasive annual grass. *Plant and Soil* 286, 153–165.
- Sigüenza, C., Crowley, D.E., Allen, E.B., 2006b. Soil microorganisms of a native shrub and exotic grasses along a nitrogen deposition gradient in southern California. *Applied Soil Ecology* 32, 13–26.
- Sirajuddin, A.T., 2009. Impact of atmospheric nitrogen pollution on belowground mycorrhizal community structure and composition in the San Bernardino Mountains. Ph.D. Dissertation, University of California, Riverside.
- Skinner, M.W., Pavlik, B.M., 1997. CNPS Inventory of Rare and Endangered Vascular Plants of California. The California Native Plant Society, Sacramento, California.
- Steers, R.J., Allen, E.B., 2010. Post-fire control of invasive plants promotes native succession in a burned desert shrubland. *Restoration Ecology*. doi:10.1111/j.1526-100X.2009.00622.x.
- Stephens, S.L., Finney, M.A., 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. *Forest Ecology and Management* 162, 261–271.
- Stevens, C.J., Dise, N.B., Mountford, J.O., Gowing, D.J., 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science* 303, 1876–1879.
- Stoddard, J.L., Traaen, T.S., Skjelkvale, B.L., 2001. Assessment of nitrogen leaching at ICP-Waters sites (Europe and North America). *Water, Air and Soil Pollution* 130, 781–786.
- Tague, C., Seaby, L., Hope, A., 2009. Modeling the eco-hydrologic response of a Mediterranean type ecosystem to the combined impacts of projected climate change and altered fire frequencies. *Climatic Change* 93, 137–155.
- Talluto, M.V., Suding, K.N., 2008. Historical change in coastal sage scrub in southern California in relation to fire frequency and air pollution. *Landscape Ecology* 23, 803–815.
- Tonnesen, G., Wang, Z., Omary, M., Chien, C.-J., 2007. Assessment of nitrogen deposition: modeling and habitat assessment. California Energy Commission, PIER Energy-Related Environmental Research. CEC-500-2006-032. Available from: <http://www.energy.ca.gov/2006publications/CEC-500-2006-032/CEC-500-2006-032.PDF>.
- UBA, (Ed.), 2004. *Manual on Methodologies and Criteria for Modelling and Mapping Critical Loads and Levels, and Air Pollution Effects, Risks and Trends*. German Federal Environmental Agency, Berlin, Germany, 190 pp. Available from: www.icpmapping.org.
- U.S. Bureau of Reclamation, Mid-Pacific Region, MPGIS Service, 1996. Digital representation of Küchler vegetation potential map for California: Natural Vegetation of California (1977) by A.W. Küchler. Original map was prepared in conjunction with the publication of Barbour, M.G., Major, J. (Eds.) 1977. *Terrestrial Vegetation of California*. California Native Plant Society, Sacramento. A printed copy of the map was included with the 1988 expanded edition of Barbour and Major.
- US Environmental Protection Agency (USEPA), 2008. National Emission Inventory Database. Available from: <http://www.epa.gov/air/data/neidb.html> (accessed 25.10.10).
- USFWS, 1998. *Recovery Plan for Serpentine Soil Species of the San Francisco Bay Area*. Portland, OR, 330+ pp.
- Van Dobben, H.F., van Hinsberg, A., Schouwenberg, E.P.A.G., Jansen, M., Mol-Dijkstra, J.P., Wieggers, H.J.J., Kros, J., de Vries, W., 2006. Simulation of critical loads for nitrogen for terrestrial plant communities in the Netherlands. *Ecosystems* 9, 32–45.
- Verburg, P.S.J., Johnson, D.W., 2001. A spreadsheet-based biogeochemical model to simulate nutrient cycling processes in forest ecosystems. *Ecological Modelling* 141, 185–200.
- Vourlitis, G.L., Pasquini, S.C., 2009. Experimental dry-season N deposition alters species composition in southern Californian Mediterranean-type shrublands. *Ecology* 90, 2183–2189.
- Wan, S., Hui, D., Luo, Y., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecological Applications* 11, 1349–1365.
- Weiss, S.B., 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology* 13, 1476–1486.
- Weiss, S.B., 2006. Impacts of nitrogen deposition on California ecosystems and biodiversity. Sacramento, CA, California Energy Commission, PIER Energy-Related Environmental Research CEC-500-2005-165. Available from: <http://www.energy.ca.gov/2005publications/CEC-500-2005-165/CEC-500-2005-165.PDF>.
- Wood, Y.A., Fenn, M., Meixner, T., Shouse, P.J., Breiner, J., Allen, E., Wu, L., 2007. Smog nitrogen and the rapid acidification of forest soil, San Bernardino Mountains, southern California. *The Scientific World Journal* 7 (S1), 175–180. doi:10.1100/tsw.2007.74.
- Zavaleta, E.S., Shaw, M.R., Chiariello, N.R., Mooney, H.A., Field, C.B., 2003. Additive effects of simulated climate changes, elevated CO₂, and nitrogen deposition on grassland diversity. *Proceedings of the National Academy of Sciences* 100, 7650–7654.
- Zink, T.A., Allen, M.F., 1998. The effects of organic amendments on the restoration of a disturbed coastal sage scrub habitat. *Restoration Ecology* 6, 52–58.