

13 MEDITERRANEAN CALIFORNIA

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13.1 Ecoregion Description

The Mediterranean California ecoregion (CEC 1997; Fig 2.2) encompasses the greater Central Valley, Sierra foothills, and central coast ranges of California south to Mexico and is bounded by the Pacific Ocean, Sierra Nevada Mountains and Mojave Desert. The ecoregion description is adapted from CEC (1997). It is distinguished by its warm, mild Mediterranean climate, chaparral vegetation, agriculturally productive valleys, and a large population (>30 million). The Coast Ranges crest at 600 to 1200 m. The broad, flat, Central Valley is drained by the Sacramento and San Joaquin Rivers into the Sacramento Delta and San Francisco Bay. Rugged Transverse Ranges, peaking at 3506 m, border the Los Angeles basin. Soils are complex, mostly dry, and weakly developed with high calcium (Ca) concentrations. Summers are hot and dry (>18 °C), winters are mild (>0 °C) with precipitation from winter Pacific Ocean storms; coastal fog is common May through July. Annual precipitation (200 to 1000 mm) is highly variable and droughts are common. Vegetation is characterized by chaparral, patches of oak woodland, grassland, and some coniferous forest on upper mountain slopes. The chaparral has thickened, hardened foliage resistant to water loss and forms a cover of closely spaced, mostly evergreen shrubs 1 to 4 m tall. Common shrubs include chamise (*Adenostoma fasciculatum*), buckbrush (*Ceanothus cuneatus*), and manzanita (*Arctostaphylos* spp.). Coastal sagebrush (*Artemisia californica*) and summer-deciduous plants that tolerate more xeric conditions are found at lower elevations. A blue oak-California foothills pine (*Quercus douglasii*-*Pinus sabiniana*) woodland community forms a ring around the Central Valley, which once had extensive grasslands and riparian forests. The southern oak woodland extends into the Transverse and Peninsular Ranges and includes Southern California walnut (*Juglans californica*) and Engelmann oak (*Quercus engelmannii*). Mixed-conifer forests (Minnich 1999) occur at a higher elevation than chaparral and include a variety of species

mixes depending on elevation and site conditions, but are typically characterized by dense mixed-aged stands composed of coniferous (pine [*Pinus* spp.] and often fir [*Abies* spp.] and incense cedar [*Calocedrus decurrens*]) and broadleaved species (commonly oaks).

13.2 Coastal Sage Scrub

13.2.1 Ecosystem Description

Coastal sage scrub 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 United States portion of coastal sage scrub covers some 684,000 ha (CDFP 2007). Coastal sage scrub is very diverse. Unfortunately, it is subject to extensive human impacts in rapidly developing coastal California. Dominant species throughout the range are coastal sagebrush (*Artemisia californica*), Eastern Mojave buckwheat (*Eriogonum fasciculatum*), sage (*Salvia* spp.), brittlebush (*Encelia* spp.), and other shrub species, with highest shrub diversity occurring in the southern range. The forbs, primarily annual, are especially diverse, with many species of concern under the Endangered Species Act occurring throughout the range of coastal sage scrub in California.

13.2.2 Ecosystem Responses to N Deposition

Ecosystem responses to elevated nitrogen (N) in coastal sage scrub include increases in exotic invasive annual grasses, loss of native shrub and forb cover, reduced diversity of native annual forbs and arbuscular mycorrhizal fungi, and elevated N mineralization. Plants in this low-productivity ecosystem respond quickly to N; thus changes in species abundance are excellent indicators of ecosystem response to N pollution. This is unlike ecosystems with long-lived vegetation, such as forests or chaparral, where initial ecosystem responses to N are measured by changes in biogeochemical cycling or nutrient runoff (Aber et al. 1989, Section 13.3.3).

13.2.3 Range of Ecosystem Responses Observed

Studies along anthropogenic N deposition gradients and in experimental N-fertilized plots have shown alterations in soil N cycling, plant cover and diversity, and arbuscular mycorrhizal fungi. Nitrogen cycling studies include field and laboratory N mineralization measurements that show higher turnover of inorganic N under high N deposition or fertilization (Sirulnik et al. 2007, Vourlitis et al. 2007a, Vourlitis et al. 2007b). Plant cover and diversity studies were done along an N deposition gradient and show threshold losses of native annual forb species of 45 percent (a decrease from 67 to 37 species per site) under 10 kg N ha⁻¹ yr⁻¹ of modeled and 7.8 kg ha⁻¹ yr⁻¹ measured N deposition.¹⁵ A study of arbuscular mycorrhizal fungi was made on the same gradient and showed similar threshold losses of mycorrhizal root infection and diversity at many of the same sites showing plant loss under 9 kg N ha⁻¹ yr⁻¹ of modeled N deposition (Egerton-Warburton and Allen 2000), as described below.

Nitrogen mineralization and nitrification. Several fertilization studies conducted in coastal sage scrub used high levels of N fertilizer, 50 to 60 kg N ha⁻¹ yr⁻¹ (Allen et al. 1998, Vourlitis et al. 2007a). However, two studies on N mineralization (production of ammonium (NH₄⁺) and nitrate (NO₃⁻)) along an N deposition gradient in coastal sage scrub showed increased rates of N mineralization in soils receiving 10 compared to 4 kg N ha⁻¹ yr⁻¹ (Vourlitis et al. 2007b, Vourlitis and Zorba 2007). Another field experiment (Sirulnik et al. 2007) tested the effects of elevated N on net N mineralization and nitrification in coastal sage scrub in sites with modeled (14.7 and 8.7, as modeled by Tonnesen et al. [2007]) and inferential (20.2 vs. 6.6 kg N ha⁻¹ yr⁻¹; Table 13.3) N deposition rates. Few changes in N mineralization were observed, but nitrification (production of NO₃⁻) was significantly higher in high deposition than control plots on at least one date in all 3 years (Sirulnik et al. 2007). Because the studies by Vourlitis et al. (2007b) and Vourlitis and Zorba (2007)

detected changes in soil N dynamics at a lower level of N deposition (10 versus 4 kg N ha⁻¹ yr⁻¹) than the study by Sirulnik et al. (2007) (20.2 versus 6.6 kg N ha⁻¹ yr⁻¹), the former are used to report the N deposition response threshold for mineralization.

Vegetation cover and species richness. Coastal sage scrub is subject to levels of total N deposition up to 20 kg ha⁻¹ yr⁻¹, as estimated by the U.S. Environmental Protection Agency's Community Multiscale Air Quality (CMAQ) model (Tonnesen et al. 2007) in inland Riverside and San Bernardino Counties, an area that has been rapidly converted to exotic annual grassland in the past 30 to 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 that prevents establishment of native shrubs (Allen et al. 1998, Minnich and Dezzani 1998, Talluto and Suding 2008).

Vegetation-type conversion studies in coastal sage scrub have examined patterns of vegetation change, but have not determined the N deposition response threshold. Research in the adjacent North American Deserts ecoregion related N deposition, exotic grass biomass, and fuel for fire to determine the N deposition response threshold (Fenn et al. 2010, Rao et al. 2010, Chapter 12).

A field survey in 2003¹⁵ determined the effects of N on the native and exotic vegetation along a gradient of seven sites that ranged in N deposition from 8.7 to 19 kg N ha⁻¹ yr⁻¹ (Fenn et al. 2010; Table 13.1). Nitrogen deposition values reported are modeled wet plus dry deposition on a 4-km grid (Tonnesen et al. 2007). In addition, inferential calculations of N deposition are reported for three sites (Table 13.1). The inferential method is used to calculate dry deposition to surfaces (plant canopies and soil) based on atmospheric concentrations of N pollutants, the deposition velocities of each pollutant, surface areas, and other factors (Fenn et al. 2009). Measurements of air quality, soil N, and short-term deposition to leaf surfaces (Padgett et al. 1999) confirm this air pollution gradient. Extractable soil N (NO₃⁻ plus NH₄⁺) ranged from 10 µg g⁻¹ at the low end of the N gradient to 38 µg g⁻¹ at the high

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Table 13.1—Percent cover and richness (per 3 ha) of plant groups along an N deposition gradient in western Riverside County, California. Sites are arranged from north to south along an urban to rural gradient. Forb species richness in bold shows a rapid drop in richness, suggesting a critical load of 10 kg N ha⁻¹ yr⁻¹ by the CMAQ model (between 9.0 and 11.1 kg N ha⁻¹ yr⁻¹), and 7.8 kg N ha⁻¹ yr⁻¹ by the inferential method (between 6.6 and 8.9 kg N ha⁻¹ yr⁻¹).

Site	Exotic grass % cover	Native forb % cover	Shrub % cover	Native forbs no. of species per 3 ha	soil N μg g ⁻¹	N deposition kg N ha ⁻¹ yr ⁻¹	
						CMAQ ^a	Inferential ^b
Jurupa Hills	63.5	4.0	2.2	16	37.7	19.6	
Box Springs	69.2	18.5	2.4	31	32.6	14.7	20.2
Botanic Garden	36.0	25.4	0.2	20	28.9	13.4	
Lake Perris	0.5	26.1	2.8	30	20.3	11.1	
Mott Reserve	6.7	14.3	11.2	37	30.6	11.1	8.9
Lopez Canyon	11.1	19.6	19.3	67	9.6	9.0	6.6
Tucalota Hills	1.5	35.7	35.0	50	10.5	8.7	

^aN deposition using the CMAQ model is reported as modeled wet plus dry deposition (Tonnesen et al. 2007).

^bDeposition calculated with the inferential method also includes wet plus dry deposition to vegetation and soil; see footnote 20 on page 161.

end. Percentage cover of exotic grasses was positively correlated with soil N and atmospheric N deposition, while percentage cover of native shrubs and forbs was inversely correlated with N deposition ($P < 0.001$). Native forb richness ranged from 67 to 16 species across the deposition gradient; the rapid drop in native forb richness from 67 to 37 species per site between 9 and 11 kg N ha⁻¹ yr⁻¹ indicates impacts on plant community richness occur at 10 kg N ha⁻¹ yr⁻¹. Chosen sites had not burned in the previous 10 years, and were thus in a similar successional stage. However, the high deposition sites (modeled as 13 to 19 kg N ha⁻¹ yr⁻¹) have a history of two or more fires since the 1960s, while the low deposition sites (8 to 11 kg N ha⁻¹ yr⁻¹) have burned only once since the 1960s. The two sites with deposition of 11 kg N ha⁻¹ yr⁻¹ have reduced native cover and richness even without frequent fires, which suggests a direct effect of N on native species, such as increased competition by nitrophilous exotic grasses (Yoshida and Allen 2004).

Arbuscular mycorrhizal fungi. Both mycorrhizal root infection and mycorrhizal spore species density decreased greatly between 8.7 and 9.6 kg N ha⁻¹ yr⁻¹ of modeled N deposition (Tonnesen et al. 2007) along the same N deposition gradient reported above in coastal sage scrub vegetation in southern California

(Egerton-Warburton and Allen 2000, Fenn et al. 2010). The decrease in mycorrhizal fungi occurred between inferential values of 6.6 and 8.9 kg N ha⁻¹ yr⁻¹; inferential values were not available for all sites (Table 13.2). Mycorrhizal root infection indicates the extent to which plants may depend on mycorrhizae for their nutrient uptake, and is typically reduced in extent by elevated soil nutrients, while spore density is an indication of the amount of carbon flowing from the plant to the fungus and indicates the strength of the mutualistic relationship.

13.2.4 Estimated Critical Loads

A summary of critical loads for ecosystem responses in coastal sage scrub is given in Table 13.3. Given the rapid decrease in native species cover and forb richness between 9 and 11 kg N ha⁻¹ yr⁻¹, 10 kg N ha⁻¹ yr⁻¹ may be estimated as the critical load for loss of native diversity and cover in coastal sage scrub based on modeled N deposition, while 7.8 kg N ha⁻¹ yr⁻¹ may be calculated using inferential data (Table 13.1). Percent colonization and spore counts of arbuscular mycorrhizal fungi in coastal sage scrub decline steeply at deposition levels of 9.2 kg N ha⁻¹ yr⁻¹ using the modeled data and 7.8 kg N ha⁻¹ yr⁻¹ using inferential data at many of the same sites. A critical load for loss of arbuscular mycorrhizal activity is estimated at 9.2 kg

Table 13.2—Spore counts and percent root infection of arbuscular mycorrhizal fungi along an N deposition gradient in western Riverside County, California. Sites are arranged from north to south along an urban to rural gradient (data from Egerton-Warburton and Allen 2000). Values in bold show a change in spore density and root infection and are interpreted to represent a critical load.

Site	Spores/g soil	% root infection	soil N $\mu\text{g g}^{-1}$	N deposition $\text{kg N ha}^{-1} \text{yr}^{-1}$	
				CMAQ ^a	Inferential ^b
Jurupa Hills	23	19	86.2	19.6	
Waterman Rd.	54	18	15.6	16.9	
Box Springs Mt.	66	17	26.4	14.7	20.2
Mockingbird Cyn	74	24	56.8	12.5	
Lake Mathews	70	23	39.5	11.1	
Motte Reserve	80	27	26.1	11.1	8.9
Hemet	78	22	12.8	9.6	
Lake Skinner	103	39	7.5	8.7	6.6
Santa Margarita	105	45	9.7	8.7	

^aN deposition using the CMAQ model is reported as modeled wet plus dry deposition (Tonnesen et al. 2007).

^bDeposition calculated with the inferential method also includes wet plus dry deposition to vegetation and soil; see footnote 20 on page 161.

$\text{N ha}^{-1} \text{yr}^{-1}$ using modeled data, and $7.8 \text{ kg N ha}^{-1} \text{yr}^{-1}$ using the inferential method (inferential data are not available for all modeled areas). The addition of more sample sites to the analysis along the gradient allows more precise values of critical loads to be estimated, as in the case of modeled N for mycorrhizal fungi. One challenge in setting critical loads for this system is that the lowest modeled N deposition is $8.7 \text{ kg N ha}^{-1} \text{yr}^{-1}$, and the lowest value for the inferential method is $6.6 \text{ kg N ha}^{-1} \text{yr}^{-1}$, values that are already significantly elevated above pre-industrial background deposition. Therefore, the critical load as defined from our study should be considered an upper limit. The threshold might actually be lower than these values. The critical load, with the limitations described above, is considered fairly reliable.

13.3 Chaparral and Oak Woodlands and the Central Valley

13.3.1 Ecosystem Description

Chaparral and oak woodland ecosystems are widespread over the Mediterranean California ecoregion. In this section, the term chaparral refers specifically to California chaparral, an ecosystem type composed of evergreen shrublands occupying most of the hills and lower mountain slopes of California. Chaparral has no

commercial value, yet it forms an important cover that helps maintain the integrity of the watershed. Chaparral encompasses about 2.5 million ha, or 6.1 percent of the state (Keeley and Davis 2007). Shrubs common to chaparral include manzanita, *Ceanothus* (California lilac; *Ceanothus* spp.), buckbrush, chamise, and toyon (*Heteromeles arbutifolia*). Hardwood woodlands include several species of deciduous and live oaks (*Quercus* spp.), box elder (*Acer negundo*) and big leaf maple (*Acer macrophyllum*), California buckeye (*Aesculus californica*), California ash (*Fraxinus latifolia*), Oregon ash (*Fraxinus latifolia*), southern California walnut, and Fremont cottonwood (*Populus fremontii*). Occasional conifers are California foothill pine and Douglas-fir (*Pseudotsuga menziesii*). The Central Valley, now largely converted to agricultural production, was chiefly a grassland and forbland ecosystem, with riparian belts of hardwood trees (CEC 1997) and expansive tule (*Schoenoplectus acutus*) sedge wetlands along rivers and streams (Munz 1973).

13.3.2 Ecosystem Responses to N Deposition

Chaparral ecosystem responses to N deposition include elevated NO_3^- leaching in streamwater and nitric oxide (NO) emissions from soil, increased direct transport

Table 13.3—Empirical critical loads of nutrient N for coastal sage scrub ecosystems of the Mediterranean California ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Critical load for N deposition ^a kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Coastal sage scrub, W. Riverside Co.	7.8-10	#	Increase in exotic grass cover, decrease in native richness and cover	See Table 13.1	Allen unpublished ^b ; Fenn et al. 2010
Coastal sage scrub, W. Riverside Co.	7.8-9.2	#	Decrease in arbuscular-mycorrhizal spore density, richness, and percent root infection	Table 13.2	Egerton-Warburton and Allen 2000; Fenn et al. 2010
Coastal sage scrub, W. Riverside Co.	10	#	Increase in N mineralization rate	Comparison of sites with 4 and 10 kg N ha ⁻¹ yr ⁻¹ deposition	Vourlitis and Zorba 2007, Vourlitis et al. 2007b

^aN deposition is modeled as total wet plus dry N (Tonnesen et al. 2007)

^bSee footnote 15 on page 144

of atmospheric NO₃⁻ from polluted catchments, N enrichment of soil and vegetation, increased N cycling rates in soil, and decreased diversity, species richness, and productivity of arbuscular mycorrhizal communities. In chaparral and oak woodlands, lichen communities have been severely altered by N deposition. Elevated NO₃⁻ leaching often follows high atmospheric N inputs to the catchment due to limited biological assimilation or retention. The N response of chaparral ecosystems is not known to be confounded by co-occurring ozone (O₃) effects as it is in forested areas (see section 13.4). Chaparral vegetation is highly O₃ tolerant (Stolte 1982, Temple 1999), and even if some species were O₃ sensitive, California chaparral vegetation is quiescent in summer, when O₃ levels are high.

Factors predisposing both California chaparral and forests to N loss are the active nitrifying characteristics of the soils (Fenn et al. 1998, Fenn et al. 1993, Riggan et al. 1985, Vourlitis and Zorba 2007). Chaparral soils exposed to chronic N deposition exhibit elevated N cycling, as evidenced by lower carbon:nitrogen (C:N) ratios, higher N mineralization rates, and increased δ¹⁵N (Vourlitis and Zorba 2007). The high nitrification capacity of these soils is evidenced by virtually complete net nitrification of mineralized N. Although N responses at low to moderate N input levels have not been evaluated in grasslands in the Central Valley, N deposition in serpentine grasslands near San Jose, California, has been shown to cause the displacement

of native herbaceous species by exotic invasive annual grasses (Weiss 1999).

13.3.3 Range of Ecosystem Responses Observed

Data on N deposition effects on chaparral are primarily available from the south coast (Los Angeles) air basin and a watershed study in Sequoia National Park in central California. Although short-term N addition studies have been done, little is known about the long-term effects of N enrichment on vegetation.

Nitrate leaching and nitrification. Because of the virtually complete nitrification of mineralized N in chaparral and forested soils in southern California, approximately 95 percent of the inorganic N in soil occurs in the form of NO₃⁻ (Fenn et al. 1998, Fenn et al. 1993, Vourlitis et al. 2007b). Nitrification in chaparral and coastal sage scrub soils increases in response to nitrogen deposition (Vourlitis et al. 2007b). Data relating atmospheric deposition and streamwater NO₃⁻ in chaparral watersheds are available for three areas of California: in several catchments in the San Dimas Experimental Forest, located in the San Gabriel Mountains 45 km northeast of Los Angeles; eight streams in the Devil Canyon watershed, in the western San Bernardino Mountains; and Chamise Creek, a catchment located along the southwestern slope of the Sierra Nevada Mountains within Sequoia and Kings Canyon National Parks (Fenn et al. 2003b). In addition, 56 chaparral streams were sampled for NO₃⁻ concentrations in a

regional survey in March 1982 across the greater Los Angeles Basin and in northern San Diego County over a wide range of N deposition exposures, demonstrating the relationship between N deposition and NO_3^- concentrations in streamwater in these ecosystems (Riggan et al. 1985).

Over 20 years of atmospheric deposition and streamwater NO_3^- data are available from San Dimas Experimental Forest watersheds (Meixner et al. 2006; Riggan et al. 1985, 1994). Atmospheric and streamwater NO_3^- data over shorter periods are available from Devil Canyon (Fenn and Poth 1999, Meixner and Fenn 2004). The Chamise Creek watershed was sampled continuously from 1983 to 1998 (Fenn et al. 2003a). In all three of these study areas, the catchments can be considered to be at Stage 2 of Stoddard's watershed N saturation model (Stoddard 1994) based on the seasonal NO_3^- export patterns and peak NO_3^- concentrations. More information on N saturation can be found in Chapter 1.

Nitrate concentrations in streamwater from chaparral watersheds in California are the highest reported from North America; peak concentrations greater than 200 to 300 $\mu\text{eq L}^{-1}$ are common in catchments receiving elevated N deposition while peaks as high as 700 $\mu\text{eq L}^{-1}$ have been reported (Fenn et al. 2003a, 2003b; Fenn and Poth 1999; Riggan et al. 1985, 1994). On the other hand, total NO_3^- export is often less than in N saturated mesic forests, presumably because of the high evapotranspiration fluxes relative to annual precipitation inputs. Nitrogen export in N-saturated chaparral catchments typically ranges from 1 to 10 $\text{kg ha}^{-1} \text{yr}^{-1}$, varying greatly from year to year because of highly variable precipitation (Fenn and Poth 1999, Riggan et al. 1985).

The proportion of NO_3^- exported from chaparral catchments in the Transverse Ranges of southern California that was direct throughput of atmospheric NO_3^- (e.g., without biological assimilation or retention within the watersheds) was quantified using a state-of-the-art isotopic method developed at the University of California in San Diego ($\Delta^{17}\text{O}$ as a tracer for

atmospheric NO_3^-) (Michalski et al. 2004). During peak flow following storm events, about 40 percent of the stream NO_3^- was found to originate from atmospheric sources that are transported through the watershed without any prior biological assimilation. All soil and aquatic NO_3^- samples in the study had positive $\Delta^{17}\text{O}$ values, unambiguously showing that every sample of soil and water (including groundwater) collected exhibited a signal of direct atmospheric NO_3^- inputs (Michalski et al. 2004), thus highlighting the N-saturated condition of these catchments. Nonetheless, on average, only about 10 percent of total N deposition is exported in streamwater from N-saturated catchments in the San Dimas Experimental Forest and in Devil Canyon (Fenn and Poth 1999, Meixner and Fenn 2004, Meixner et al. 2006, Riggan et al. 1985).

Trace gas losses of N. Nitrogen-saturated chaparral ecosystems also exhibit trace N gas emissions, primarily as NO, but nitrous oxide (N_2O) emissions can also be quantitatively important during the relatively short periods when soils are sufficiently wetted (Anderson and Poth 1989). In more anaerobic zones of the groundwater system and near riparian zones, losses of reduced N gases are also expected to be important in N saturated chaparral catchments. Fluxes of NO from soil over a 6-month period from July to December 1986 were estimated to be 1 kg N ha^{-1} in an unburned site and 3 kg N ha^{-1} in a burned chaparral site in the San Dimas Experimental Forest (Anderson and Poth 1989). Data are not available on trace gas losses from the near-riparian zone, or from phreatic zones in chaparral or forested watersheds in California with elevated N deposition. However, very high levels of dissolved N_2O were found in groundwater samples collected from a fault line (Fenn and Poth 1999) within the chaparral zone of the N-saturated Devil Canyon watershed.¹⁶ This pattern suggests that large amounts of excess N may be lost from these catchments via degassing of dissolved N trace gases (Bowden and Bormann 1986).

¹⁶Fenn, M.E. Unpublished data. Research plant pathologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

Fire effects on N losses. Ecosystem responses to chronic N deposition must be considered within the context of regular fire occurrence in chaparral. Stand-replacing fire return intervals in these ecosystems are generally on the order of 40 to 60 years (Minnich and Bahre 1995). Over time, N from atmospheric deposition accumulates in soil, organic matter, necromass, and biomass. During a burn, much of the N in the aboveground N-enriched vegetation and detritus is released to the atmosphere or deposited on the soil surface, where it is mobilized via nitrification, N trace gas emissions, NO_3^- leaching, and erosion, thus resulting in large pulses of N losses (Anderson and Poth 1989, Riggan et al. 1994). Such losses are of much shorter duration and are more muted in burned chaparral catchments not exposed to elevated N deposition (Riggan et al. 1985, 1994). However, fire removes only a minor component of the large N pools in the mineral soil. As a result, a large pool of N remains in the ecosystem even after a stand-replacing fire. This, combined with continuing atmospheric inputs, results in continued long-term elevated NO_3^- leaching in surface runoff and groundwater (Meixner et al. 2006). Thus, fire alone does not appear to be an effective tool for mitigating N saturation, although simulation studies suggest that N losses from higher elevation forested regions can be mitigated if N deposition is decreased and prescribed fire is applied periodically (Gimeno et al. 2009).

Soil acidification. The pH of chaparral soils measured at more than 700 San Gabriel Mountain sites in the 1970s was compared to measurements taken at more than 300 sites in the 1990s. Surface soil pH values decreased considerably over this period (Wood et al. 1992). Values of pH in the 1970s typically ranged from 6.0 to 7.4 compared to a typical range of 4.6 to 5.6 in the 1990s.¹⁷

Arbuscular mycorrhizal fungi. In a retrospective study from the San Dimas Experimental Forest, historical trends in biodiversity of the arbuscular mycorrhizal community were evaluated in pure stands of Eastern Mojave buckwheat and chamise established in the

1940s on a homogenized fine sandy loam soil (Egerton-Warburton et al. 2001). This analysis was done by evaluating the diversity of arbuscular mycorrhizal fungal spores in archived soils collected periodically from 1937 to 1999, and from examinations of mycorrhizae on root samples in 1999. It was observed that N enrichment of the soils increased over the same period in which mycorrhizal communities experienced dramatic changes (Egerton-Warburton et al. 2001). Diversity, species richness, and productivity of the arbuscular mycorrhizal community had deteriorated severely by 1969. Three previously common mycorrhizal genera disappeared from the mycorrhizal spore community in soil, and one large-spored genus (*Gigaspora*) was no longer found in the rhizosphere soil. Nitrogen enrichment also enhanced the proliferation of potentially less mutualistic species of small-spored *Glomus*, which may have implications for plant community succession in the face of chronic N deposition (Egerton-Warburton et al. 2001). Throughfall N fluxes in the San Dimas Experimental Forest in the early 1980s were $23 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Riggan et al. 1985) and total deposition was estimated at $35 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Meixner et al. 2006).

Lichen responses. About half the epiphytic lichen species known to occur during the late 1800s and early 1900s on coast live oak throughout the chaparral and oak vegetation zones of the Los Angeles basin (Hasse 1913) have subsequently disappeared (Ross 1982). This dramatic reduction in species richness was initially attributed solely to oxidizing pollutants, chiefly O_3 (Nash and Sigal 1999, Ross and Nash 1983), but recent research provides unequivocal evidence for an N deposition effect (Riddell et al. 2008). In the Los Angeles air basin, throughfall N deposition in forests downwind of the urban areas can reach $25 \text{ to } 70 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Fenn et al. 2008). This deposition includes nitric acid (HNO_3), a strong gas-phase acid which exhibits diurnal patterns paralleling O_3 concentrations. In the mountains downwind of Los Angeles, 24-hr means of up to 27.3 ppb have been recorded, whereas remote location means have been $\leq 0.1 \text{ ppb}$ (Bytnerowicz and Fenn 1996). Unlike O_3 , once HNO_3 is produced, it rapidly deposits to surfaces. Menzies' cartilage lichen (*Ramalina menziesii* Tayl.), a dominant epiphyte of oaks throughout the Coast Ranges of California and

¹⁷Wood, H.B. Unpublished data on file with Mark Fenn, Research plant pathologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

historically common in the Los Angeles basin (Hasse 1913) was treated with nitric acid at 7 to 25, and 19.9 to 25 $\mu\text{g m}^{-3}$ during month-long fumigations to mimic diurnal patterns in Los Angeles (Riddell et al. 2008). All specimens in both treatments experienced marked declines in chlorophyll content, carbon exchange capacity, and membrane integrity compared to controls. In addition to oxidant and acidic air pollutants, Riddell et al. (2008) also recognized habitat loss, lower humidity due to urbanization, and increased fire incidence as factors in the disappearance of Menzies' cartilage and other lichens from the Los Angeles basin.

Epiphytic lichen communities in more northerly parts of the ecoregion are also showing a clear response to N. The Greater Central Valley, comprising the Central Valley proper and the surrounding chaparral- and oak woodland-dominated central Coast Ranges and Sierra foothills, encompasses many urban centers and is among the most agriculturally intensive regions of the United States. Using a nonmetric multidimensional scaling procedure and vector overlays of environmental variables, Jovan and McCune (2005) ordinated and scored lichen communities surveyed between 1998 and 2001 at 118 sites in the Greater Central Valley along an NH_3 emissions gradient (Fig. 13.1). There were strong correlations between NH_3 and percentages of eutrophic lichen richness and abundance. In addition, total N deposition and other N species, including HNO_3 , NO_3^- , and NO_2 , were all positively correlated with lichen scores, suggesting that multiple N-containing compounds, not just NH_3 , are impacting lichens in the Greater Central Valley (Jovan 2008). Eutrophic lichens benefited from increasing N availability, comprising >50 percent of total abundance in lichen communities at air scores <0.0 (Fig. 13.2). Higher air scores indicate better air quality. Eutroph abundance at sites with the best air quality ranged from 20 to 50 percent. Therefore an air score of 0.0 may be a reasonable lichen response threshold. CMAQ data were not available to the authors at the time of publication, but overlay of a 4-km grid of modeled 2002 CMAQ data (Tonnesen et al. 2007) over lichen survey site coordinates provides a more complete understanding of N deposition at the Jovan and McCune (2005) sites. Of the 53 lichen survey sites in the dataset with clean air scores (>0.0), only three

occurred in grid cells where CMAQ predicted >5.5 $\text{kg ha}^{-1} \text{yr}^{-1}$ total N deposition.

13.3.4 Estimated Critical Loads

In chaparral catchments exhibiting the symptoms of N excess discussed above, N input values range from 5 to 33 $\text{kg ha}^{-1} \text{yr}^{-1}$ as throughfall (Meixner and Fenn 2004), except for the case of the chaparral/oak woodland lichen response studies in the greater Central Valley, where N deposition was simulated with the CMAQ model (Tonnesen et al. 2007). In the seven catchments sampled in Devil Canyon, throughfall N deposition ranged from 14 to 33 $\text{kg ha}^{-1} \text{yr}^{-1}$. Because all seven sites had elevated NO_3^- concentrations in stream water, the lowest deposition value can be considered to be at or above the critical load. Chamise Creek in Sequoia National Park is an N-saturated site based on elevated NO_3^- leaching (Fenn et al. 2003a, 2003b); throughfall N deposition¹⁸ was 10 $\text{kg ha}^{-1} \text{yr}^{-1}$. Lichen survey sites with clean air scores suggest a preliminary critical load of 5.5 $\text{kg N ha}^{-1} \text{yr}^{-1}$. In a test of the broader applicability of a model developed from western Oregon and Washington lichen community data to temperate forests in general, Geiser et al. (2010), essentially replicated this estimate. For the Greater Central Valley dataset (Jovan and McCune 2005) and response threshold (50 percent eutrophs), Geiser et al. (2010) calculated a critical load of 3 to 6 $\text{kg N ha}^{-1} \text{yr}^{-1}$ for the study area, increasing with mean annual precipitation from 17 to 156 cm. An N critical load for serpentine grassland invasion by exotic annual grasses was determined along a roadside deposition gradient at a site downwind of San Jose, California, and west of the Central Valley. The critical load of 6 $\text{kg N ha}^{-1} \text{yr}^{-1}$ was based on the N deposition level at the point where the grass invasion was visibly diminished (Fenn et al. 2010, Weiss 1999). Considering the deposition and response data from all the ecosystem components considered here, we suggest a deposition range for the critical load of 3.1 to 14 $\text{kg N ha}^{-1} \text{yr}^{-1}$. All the reported responses (see Table 13.4) occur within this range.

¹⁸Homyak, P.M. 2009. Personal communication. Graduate research associate, Department of Environmental Sciences, University of California, Riverside, CA 92521.

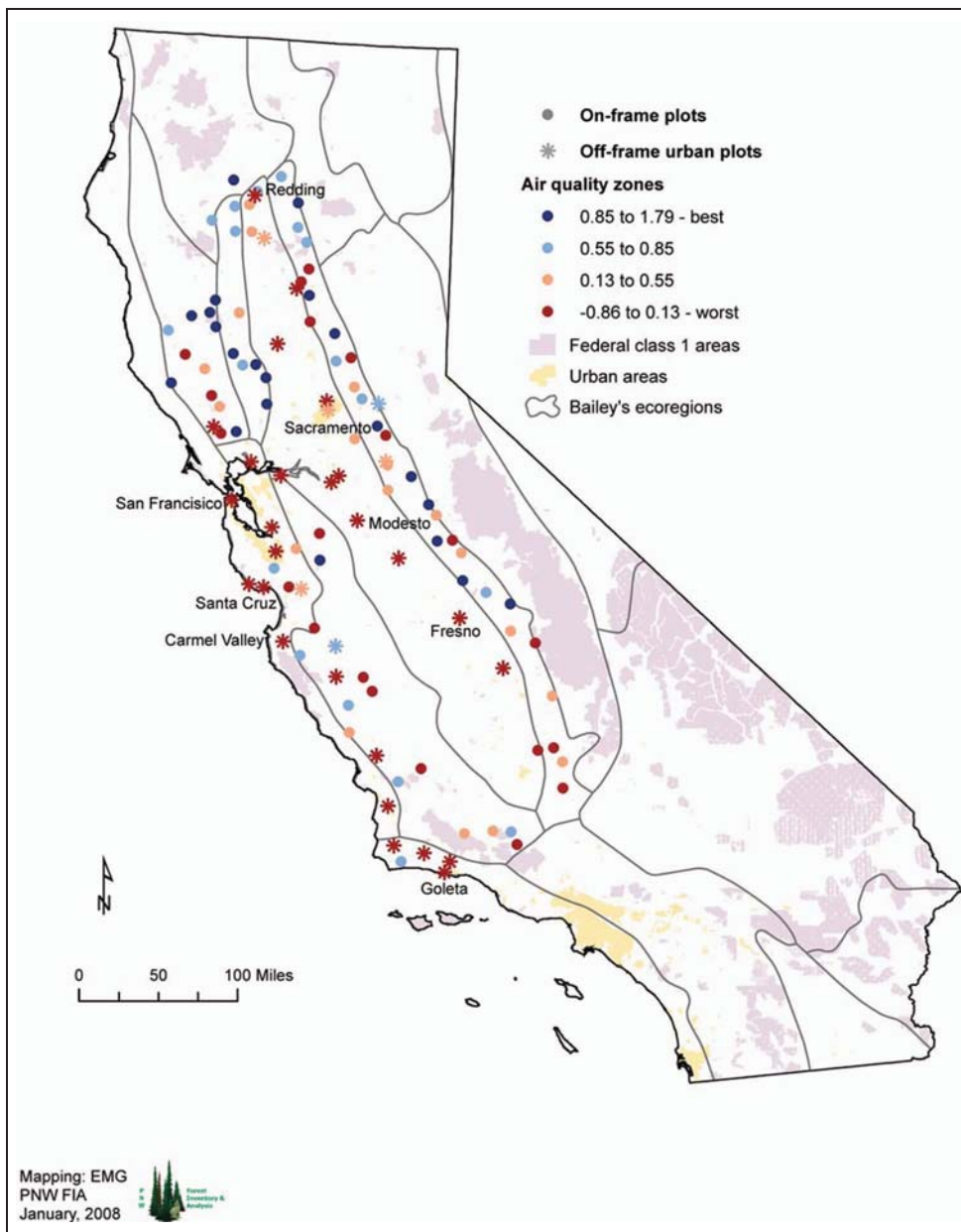


Figure 13.1—Air quality scores for the greater Central Valley divided into air quality zones. Reprinted from Jovan 2008.

In the San Dimas Experimental Forest, with a reported throughfall N deposition of $23 \text{ kg ha}^{-1} \text{ yr}^{-1}$, the critical load is exceeded for NO_3^- leaching, changes in mycorrhizal spore community changes, and elevated NO emissions from soil. The critical load for NO_3^- leaching is known to be much lower than the deposition at San Dimas as discussed above, but the critical load for mycorrhizal community changes and for N trace gas emissions cannot be determined because we only have data from San Dimas. Likewise, the critical load for increased nitrification has not been established due to insufficient corresponding deposition data at sites where

nitrification has been measured. Thus, the critical load for these responses are not included in the critical loads tables.

13.4 Mixed-conifer Forest

13.4.1 Ecosystem Description

Air pollution effects studies in California forests have focused largely on the mixed-conifer forests found at mid-elevation sites in the Transverse Ranges (particularly the San Bernardino Mountains) in the Los Angeles air basin and in the southwestern Sierra Nevada (Fenn et al. 2003b). Because of the high sensitivity to

Table 13.4—Empirical critical loads of nutrient N for chaparral and Central Valley ecosystems of the Mediterranean California ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Critical load for N deposition ^a kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Sacramento & San Joaquin Valleys, Coast Ranges & Sierra Foothills	3-6	#	Change in lichen communities	Shift to eutroph dominance, precipitation range of 17-156 cm.	Geiser et al. 2010
San Francisco Peninsula, near San Jose, California	6	##	Annual grass invasion, replacing native herbs in a serpentine grassland	Critical load based on a local roadside gradient; Serpentine grassland site is actually west of the Central Valley.	Weiss 1999, Fenn et al. 2010
Sacramento & San Joaquin Valleys, Coast Ranges & Sierra Foothills	5.5	#	Changes in lichen communities	Eutrophic lichens increased at expense of species adapted to lower N availability.	Fenn et al. 2010, Jovan and McCune 2005, Jovan 2008, this chapter
Chamise Creek, Sequoia NP	10	#	Streamwater [NO ₃] > 14 µM	This NO ₃ threshold indicates the beginning of N saturation.	Fenn et al. 2003b, Fenn et al. 2003a, Fenn et al. 2010
Devil Canyon, San Bernardino Mountains	14	#	Streamwater [NO ₃] > 14 µM	Estimated N deposition in throughfall in the 7 catchments was 14-33, so critical load is lowest value.	Meixner and Fenn, 2004, Fenn and Poth 1999, Fenn et al. 2010
Los Angeles Basin	Atmospheric concentrations of 7-25 µg HNO ₃ m ⁻³	#	Loss of lichen species richness and harm to physiological processes	About half of the 1900 lichen flora in the Los Angeles basin is currently extirpated, attributed to O ₃ and N pollutants.	Riddell et al. 2008; Hasse 1913; Ross, 1982; Sigal and Nash 1983

^aN deposition is reported as throughfall (Fenn and Poth 2004, Fenn et al. 2008) except for the serpentine grassland study and lichen studies in chaparral. In the Los Angeles Basin the range of atmospheric concentrations shown for HNO₃ indicate the concentrations at which lichens are impacted. For changes in lichen communities in the Central California valleys, coast ranges and Sierra foothills, N deposition values for determining the critical loads were simulated using the CMAQ model (Tonnesen et al. 2007). Deposition data for Chamise Creek, Sequoia National Park provided by P.M. Homyak; see footnote 18 on page 150

O₃ of ponderosa pine (*Pinus ponderosa*) and the closely related Jeffrey pine (*Pinus jeffreyi*), most of the research has been carried out in sites with a predominant component of these species. Associated tree species that co-occur in varying mixes with ponderosa and Jeffrey pine include white fir (*Abies concolor*), sugar pine, (*Pinus lambertiana*), incense-cedar, and California black oak (*Quercus kelloggii*). In parts of the southwest Sierra Nevada, Douglas-fir and giant sequoia (*Sequoiadendron giganteum*) are also found (Minnich 1999, Peterson and Arbaugh 1992). Shrub understory in mixed-conifer forest is mostly open or absent (cover <20 percent), depending on altitude and climatic gradients. Bracken fern (*Pteridium aquilinum* var. *pubescens*) is common in more mesic sites. See Minnich (1999) for a more complete description of common understory species in mixed-conifer forests.

13.4.2 Ecosystem Responses to N Deposition

Research on air pollution effects in mixed-conifer forests began in the 1960s after the initial discovery in the 1950s of unusual symptoms in ponderosa pine that were later confirmed to be caused by O₃. Studies on N deposition effects in forests began in the San Bernardino Mountains (Fenn 1991) in some of the original O₃ study plots established in the 1970s (Arbaugh et al. 2003). Ecosystem responses to N deposition include NO₃⁻ leaching, trace gas losses of N, soil acidification, lichen community change, altered forest nutrient cycling, and loss of understory diversity. Because of the co-occurrence of O₃ and N deposition in the mixed-conifer forest of California, the ecological effects of N deposition cannot be evaluated in isolation from the significant impacts of O₃ on nutrient cycling and plant growth, development, community succession, and phenology. The combined ecological effects of N and O₃ are dramatic in areas of high pollution exposure (Fenn et al. 2003b, Grulke et al. 2009).

13.4.3 Range of Ecosystem Responses Observed

Most characteristics which predispose an ecosystem to NO₃⁻ leaching (e.g., climatic conditions, actively nitrifying soils) discussed for chaparral ecosystems in section 13.3 also apply to forested catchments, as many mixed-conifer catchments grade into

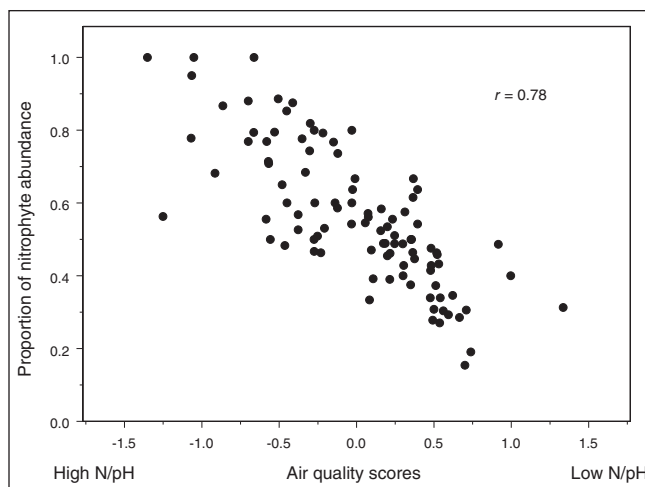


Figure 13.2—The relationship between air quality score and the proportion of nitrophyte (eutroph) abundance in California's greater Central Valley. Reprinted from Jovan 2008.

chaparral vegetation at lower elevations. Indeed, 4 of 11 catchment streams monitored to determine the relationship between N deposition and NO₃⁻ leaching in the mixed-conifer forest were accessible for sampling only at the lower elevation chaparral portion of the catchment (Fenn et al. 2008). In both chaparral and mixed-conifer forests, a key factor predisposing these ecosystems to N loss with chronic N deposition is the temporal asynchrony between the period of greatest biotic demand (spring and early summer) and the winter when approximately 85 percent of the precipitation and the greatest surface runoff occurs (Fenn and Poth 1999).

Nitrate leaching. A threshold streamwater NO₃⁻ concentration for a site experiencing relatively low atmospheric N deposition (14 μM) was empirically determined to identify watersheds that are exporting elevated levels of NO₃⁻ (see Fenn et al. 2008, 2010 for more details on these methods and rationale). Based on regression analysis of throughfall N deposition versus streamwater NO₃⁻ concentrations, the N deposition level at which NO₃⁻ leaching exceeds the “unpolluted”-site threshold is approximately 17 kg ha⁻¹ yr⁻¹ (Fenn et al. 2008). This level of N deposition has been measured in the regions of the Transverse Ranges in southern California most exposed to air pollution and along the western edge of the Sierra Nevada (Breiner et al. 2007; Fenn et al. 2008, 2010).

Although many factors affect N loss rates, the available data suggest that within a given catchment, N deposition fluxes to the higher elevation forested portions of catchments are greater than to the lower chaparral and scrub vegetation portions (Meixner and Fenn 2004). This is presumably because of the much greater surface area of forested stands, which are efficient collectors of dry and cloud water deposition, and because of greater occurrence of fog and cloud deposition at the upper levels of these catchments (Fenn et al. 2000, Meixner and Fenn 2004). However, the greater input to the forested portion of the catchment is likely counterbalanced, to some degree, by greater biotic N demand of the forest. Soil leachate and streams in the mixed-conifer zone are known to export high levels of unassimilated NO_3^- (Michalski et al. 2004). In catchments covered by mixed-conifer forests at higher elevations, NO_3^- concentrations in streamwater decrease within the lower elevation chaparral zone because of in-stream and near-stream N uptake and consumptive processes along the descending course of the stream (Meixner and Fenn 2004).

Trace gas losses of N. Fluxes of trace gas emissions from soil of N-saturated sites in the mixed-conifer forest appear to be very similar to those from N-saturated chaparral sites. Annual fluxes of NO in high N deposition chaparral and forested sites generally range from 2 to 3 kg ha⁻¹ yr⁻¹ (Anderson and Poth 1989, Fenn and Poth 2001), although there is considerable uncertainty because of temporal and spatial heterogeneity in flux measurements. Emissions from soil are higher after a burn and after soil wetting. In short-term measurements, fluxes of NO and N₂O increase markedly after soil wet-up, particularly in N saturated sites (Anderson and Poth 1989, Fenn et al. 1996). Annual flux rates are probably greater in high precipitation years than the estimates given above.

Soil acidification. Because of the Mediterranean climate and typical high base saturation of soils in semi-arid forests, the possible soil acidification effects of N deposition in California have not received nearly as much attention as the effects of N as a nutrient. However, soils have acidified at an accelerated rate in high deposition sites. At Camp Paivika in the western

San Bernardino mountains, soil pH values in the top 25 cm of soil ranged from 4.8 to 5.6 in the early 1970s, compared to recent values ranging from 3.1 to 4.3¹⁹ (Fenn and Poth 1996, Wood et al. 2007). The unusually low pH values and rapid acidification at Camp Paivika are due to high throughfall N deposition (70 kg ha⁻¹ yr⁻¹) and underlying stone lines at 40 to 60 cm and 130 to 170 cm depths which control the spatial and temporal flow of soil percolates containing high concentrations of NO_3^- . At another site with the stone lines but much lower throughfall N deposition (6 kg ha⁻¹ yr⁻¹), soil acidity was relatively constant (pH 5.1 in 1975; pH 5.0 in 2004) during the last 30 years (Wood et al. 2007).

Soil pH is highly correlated ($r^2 = 0.99$) with throughfall N deposition in the San Bernardino Mountains (Breiner et al. 2007). Based on this regression, soil pH is estimated to be 4.8 when deposition is 17 kg ha⁻¹ yr⁻¹. Soil base saturation is also much lower at high N deposition sites (30 to 80 percent) compared to low deposition sites (85 to 100 percent) in the San Bernardino Mountains¹⁹ (Fenn et al. 1996). The low pH and lower base saturation of the mineral soil does not inhibit active nitrification, but a recent study suggests that nitrification is dominated by heterotrophic nitrifiers (Jordan et al. 2005).

Ectomycorrhizal fungi. Fungal communities of ectomycorrhizae were studied from November 2005 to June 2007 at a high (71 kg N ha⁻¹ yr⁻¹; Camp Paivika) and low (7 kg N ha⁻¹ yr⁻¹; Camp Osceola) deposition site in the San Bernardino Mountains east of Los Angeles (Sirajuddin 2009). The effects of added N (150 kg ha⁻¹ yr⁻¹) within each of the plots over a 9-year period were also investigated.

Basidiomycetes tended to decline with both N fertilization and at the high N deposition plot. *Russula* (five species) and *Rhizopogon* (three species) were present at Camp Osceola, but were lost with N fertilization and were not found at Camp Paivika. *Cortinarius* spp.

¹⁹Wood, Y.A. Unpublished data on file with Mark Fenn, Research plant pathologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

also decreased with N fertilization. The exceptional basidiomycete was a *Lactarius* sp., which increased in N fertilized plots at both locations. In general, ascomycetes increased with N availability; *Cenococcum geophilum* in particular increased quite dramatically. *Wilcoxinia rehmii* was the exception, in that this ascomycete declined with N enrichment, both via deposition and fertilization. In summary, N deposition and N fertilization shifted the ectomycorrhizal fungal communities in a similar direction, toward ascomycetes. Basidiomycetes generally declined and some key species disappeared with N fertilization or deposition (Sirajuddin 2009).

Lichen responses. Lichen-based responses to N deposition for the mixed-conifer zone of the Sierra Nevada (Northwest Forested Mountains ecoregion) likely have application to the mixed-conifer zone of the Mediterranean California ecoregion, especially in the southwest Sierras and Transverse Ranges, where there was a historic species overlap. The Sierra study (Fenn et al. 2008) utilized a threshold N concentration in the wolf lichen (*Letharia vulpina* (L.) Hue), an epiphyte on tree trunks and branches, from a low N deposition site. As the threshold is exceeded with increasing N deposition, the abundance of ecologically important oligotrophic species begins to decline, shifting lichen community composition from oligotroph-dominated to mesotroph- and eutroph-dominated (Fenn et al. 2008). Oligotrophs are sensitive to even small increases in N; mesotrophs tolerate moderate inputs; eutrophs are fast growing, 'weedy' species of small ecological importance that thrive under conditions of high N availability. Lichen surveys in the Sierra Nevada mixed-conifer zone were co-located with or near throughfall deposition monitoring sites. Similar studies can no longer be done in the San Bernardino Mountains because most air pollution sensitive species have long since disappeared (Nash and Sigal 1999, Sigal and Nash 1983). In relatively low N deposition sites in the Sierras ($<3.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), oligotrophic lichen species still predominate. At a throughfall N deposition level of $5.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, the lichen community completely shifts from oligotroph to mesotroph/eutroph dominance. Oligotrophs are extirpated at $10.2 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Fenn et al. 2008). Conservation of oligotrophic species is important because they make integral contributions

to food webs, nesting material and insect habitat, and nutrient and hydrologic cycles (McCune et al. 2007).

Forest sustainability. Nitrogen deposition, in concert with O_3 injury effects, is contributing to a decrease in the sustainability of mixed-conifer forests in the San Bernardino Mountains. Nitrogen deposition increases aboveground growth of coniferous and deciduous species of the mixed-conifer forest (Fenn and Poth 2001). Ozone and increased N fertility result in decreases in both C allocation belowground and fine root biomass (Grulke et al. 1998). Ozone causes premature foliar senescence and abscission. The combined effects of O_3 and elevated N deposition are increased C storage in the bole and woody aboveground biomass and accelerated foliar turnover and litter production (Arbaugh et al. 1999). This also results in increased accumulation of C and N in the forest floor. In these O_3 -impacted and N-saturated mixed-conifer stands (N deposition $25 \text{ to } 71 \text{ kg ha}^{-1} \text{ yr}^{-1}$) (Fenn et al. 2008), aboveground N pools are much higher than in stands in areas receiving relatively low deposition (Arbaugh et al. 1999, Fenn et al. 2005, Grulke et al. 2009). For example, at an N-saturated site (N deposition $71 \text{ kg ha}^{-1} \text{ yr}^{-1}$) in the San Bernardino Mountains about 30 percent of ecosystem N is stored in the thick forest floor, compared to about 11 percent at an N-limited site (N deposition approximately $7 \text{ kg ha}^{-1} \text{ yr}^{-1}$) (Arbaugh et al. 1999, Fenn et al. 2005).

Ozone and elevated N deposition cause specific changes in forest tree C, N, and water balance that enhance individual tree susceptibility to drought, bark beetle attack, and disease, and when combined, contribute to whole ecosystem susceptibility to wildfire (Grulke et al. 2009). The N deposition levels at which these effects begin to occur are not well defined, but regression analysis indicates a 25 percent reduction in fine root biomass at $17 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Fenn et al. 2008); dramatic shifts in tree phenology and C allocation are evident at a site with N deposition of $39 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Fenn et al. 2008, Grulke and Balduman 1999). Uncharacteristically deep litter layers develop in mixed-conifer forests impacted by air pollution. Elevated O_3 and N deposition decrease the proportion of whole tree biomass in foliage and roots, the latter effect increasing tree susceptibility

to drought and beetle attack. Because both foliar and root mass are compromised, carbohydrates are stored in the bole over winter. Elevated O_3 increases drought stress by significantly reducing plant control of water loss. The resulting increase in canopy transpiration, combined with O_3 and N deposition-induced decreases in root mass, significantly increases tree susceptibility to drought stress. The combination of these effects with increased sequestration of bole carbohydrates may contribute to successful host colonization and population increases of bark beetles (Jones et al. 2004) and possible enhancement of dwarf mistletoe infections, although the latter response has not been confirmed.

Understory. Understory diversity in mixed-conifer forests in the San Bernardino Mountains in southern California was recently compared to studies done 30 years prior, in 1973 (Allen et al. 2007). Both O_3 concentrations and particularly N deposition decline from west to east along the air pollution gradient. Nitrogen deposition in throughfall ranges from 9 to 71 $kg\ ha^{-1}\ yr^{-1}$ at the understory study sites (Fenn et al. 2008). Biodiversity loss was pronounced in the sites receiving the highest N deposition and is due to the establishment of exotic invasive species that have become abundant. In three of six sites, including the two westernmost polluted sites, 20 to 40 percent of species were lost between 1973 and 2003. In the highest deposition sites, understory cover equaled 30 to 45 percent and was equally divided between native and exotic species. At lower deposition sites, understory cover was 3 to 13 percent and was dominated by native species. Because of confounding factors such as precipitation and possibly local disturbances, a simple correlation between air pollution and patterns of native and invasive species cover and richness was not found. However, observational evidence and expert opinion suggest that increased N deposition and precipitation in the westernmost sites are the primary factors contributing to reduced biodiversity and increased cover by invasive species (Allen et al. 2007).

Co-occurring O_3 may be indirectly contributing to the establishment of exotic species as well. Ozone causes premature foliage loss in pine, while N deposition stimulates foliar growth, leading to greater litter

production and accumulation in the forest floor (Fenn et al. 2003b, 2005). Many native plant species are not able to establish where dense litter accumulates. However, stickywilly (*Galium aparine*), a weedy annual with both native and introduced forms, thrives under these conditions, which include the acidified N-rich soils that underlie the thick litter layer. Portions of the high-pollution study sites in the western San Bernardino Mountains burned in October 2003. Formerly shady sites in the burned areas are now covered by exotic annual brome grasses. Subsequent clearing of dead trees and brush is further exposing the soil to invasive species (Allen et al. 2007).

13.4.4 Critical Loads Estimates

The N deposition input values for the sites included in this synthesis range from 1.2 to 71.1 $kg\ ha^{-1}\ yr^{-1}$ as throughfall, with the lowest values in the northern Sierra Nevada and the highest deposition in the western San Bernardino mountains in the Los Angeles air basin. The best defined empirical critical loads are for lichen effects, developed for forests of the Sierra Nevada, with the most protective critical load for incipient effects on lichens of 3.1 $kg\ N\ ha^{-1}\ yr^{-1}$. This lower critical load is based on the low N deposition-site threshold concentration of N (1.0 percent N) in the widespread wolf lichen; at higher tissue concentrations of N, lichen community effects begin to increase (Fenn et al. 2008). Two additional lichen-based critical loads were determined for mixed-conifer forests in California: at throughfall N deposition of 5.2 $kg\ ha^{-1}\ yr^{-1}$, oligotroph dominance shifts to mesotroph/eutroph dominance, and at 10.2 $kg\ ha^{-1}\ yr^{-1}$ oligotrophic species are extirpated. These critical load estimates are considered as reliable (Table 13.5). In applying lichens critical loads, the highest threshold—that of oligotroph extirpation—would not be used under conditions where the integrity of the lichen community was considered important. We do not include it in the summary of lichens for the U.S. (Table 19.4). Application of the western Oregon and Washington model (Geiser et al. 2010; Table 4.1) to the mixed-conifer forests yields a critical load estimate of 4 to 6 $kg\ ha^{-1}\ yr^{-1}$ over a precipitation range of 41 to 127 cm. This estimate uses the mid-range response threshold (oligotroph dominance shift) instead of the lowest threshold, as it assumes that eutrophs naturally

Table 13.5—Empirical critical loads of nutrient N for mixed-conifer forest ecosystems of the Mediterranean California ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Critical load for N deposition ^a kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Sierra Nevada range	3.1-10.2 ^b	##	Lichen community changes	Critical load of 3.1 for exceedance of a N concentration threshold in <i>Letharia vulpina</i> ; critical load of 5.2 for shift from oligotroph to mesotroph/eutroph dominance of lichen communities; critical load of 10.2 for extirpation of oligotrophs	Fenn et al. 2008, 2010
Sierra Nevada range	4-6	#	Lichen community changes	Modeled estimate using the oligotroph to mesotroph/eutroph dominance shift as response threshold and 41-127 cm precipitation range	Geiser et al. 2010
San Bernardino mountains and southern Sierra Nevada range	17	##	[NO ₃] ⁻ > 14 µM	Based on regression of throughfall vs. peak streamwater NO ₃ ⁻ concentrations. A threshold of 0.2 mg NO ₃ -N L ⁻¹ (14.3 µM) identified catchments beginning to “leak” N. Daycent simulations gave similar results	Fenn et al. 2008, 2010
San Bernardino mountains	17	#	Reduced fine root biomass	Based on regression of throughfall N deposition and fine root biomass in ponderosa pine	Fenn et al. 2008, Grulke et al. 1998
San Bernardino mountains	25.9	#	Soil acidification	Based on regression of throughfall N deposition and mineral soil H ⁺ . Soil pH of 4.6 was chosen as the critical value.	Breiner et al. 2007
San Bernardino mountains	24-33	(#)	Biodiversity of understory: percent cover and no. of species/ha	Based on plant surveys in 1970s and 2003. N deposition data: Fenn et al., 2008 and unpublished data	Allen et al. 2007
San Bernardino mountains	39	(#)	Forest sustainability	Based on dramatic shifts in plant phenology and C allocation. Caused by combined effects of O ₃ and N deposition. Leads to increased bark beetle mortality and wildfire risk. N deposition data from Fenn et al. 2008	Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004

^aN deposition is reported as throughfall for all of the critical loads in this table.

^bUtilizing this critical load value would lead to a condition where lichen community composition had shifted toward dominance by eutrophs to the exclusion of oligotrophic (N-sensitive) species. Throughout this document, we use a threshold that limits shifts toward dominance by eutrophs. Thus, the value of 10.2 kg N ha⁻¹ yr⁻¹ does not appear in the chapter summarizing the critical loads for all ecoregions (Chapter 19).

comprise up to 47 percent of native lichen communities, due to the warm climate and prevalence of hardwood substrates. The critical load which would prevent elevated NO_3^- leaching and further reductions in fine root biomass of ponderosa pine (Fenn et al. 2008) is estimated at $17 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The critical load of $17 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for reductions in fine root biomass (Table 13.5) is preliminary; data from a greater number of sites are needed to refine the critical load. However, the available information on fine root biomass responses demonstrate that when N deposition is sufficient to increase NO_3^- leaching from soil and in streamwater, undesirable physiological effects are also apparent in plants. The critical load for streamwater NO_3^- is reliable, while for fine root biomass effects a fairly reliable rating is assigned (Table 13.5).

Based on a critical mineral soil pH value of 4.6 (MacDonald et al. 2002), an empirical critical load of $26 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ was also estimated and considered to be fairly reliable (Table 13.5), but the basis of this critical pH value has a tenuous connection to any firm ecosystem-specific biological or ecological effects or responses (Breiner et al. 2007, Wood et al. 2007). The estimated critical loads of 24 to $39 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, which would maintain forest sustainability and biodiversity in the understory community, are included in Table 13.5 and are only established as expert judgment. These are uncertain, as few data are available from research sites in the case of forest sustainability (Grulke and Balduman 1999, Grulke et al. 1998, Jones et al. 2004) and because of confounding factors in regard to understory biodiversity (Allen et al. 2007). The critical load for effects on ectomycorrhizal communities in California forests cannot be determined from current data because only two sites and a high N treatment level ($150 \text{ kg ha}^{-1} \text{ yr}^{-1}$) were studied (Sirajuddin 2009).

13.5 Critical Loads Comparisons Across Ecosystem Types

The lowest critical load estimated for these California Mediterranean ecosystem types (Table 13.6) was $3.1 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for the mixed-conifer forest. This value is based on the throughfall N deposition input leading to N concentrations in lichen thalli (*Letharia vulpina*) of the

Sierra Nevada that exceed that of the low N deposition site threshold (Fenn et al. 2008). At a throughfall N deposition critical load of 3.5 to $5.9 \text{ kg ha}^{-1} \text{ yr}^{-1}$ the lichen community in mixed-conifer forests is predicted to shift from oligotroph dominance to mesotroph/eutroph dominance. The lichen community responses to simulated N deposition resulted in a critical load of 3.1 to $6.4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for chaparral, oak woodland, and Central Valley lichen communities. Lichen communities of coastal sage scrub have not been studied with regard to air pollution effects. Thus, lichens are not yet an available bioindicator in coastal sage scrub.

The critical load for invasion of annual grasses in a nutrient-poor serpentine grassland ($6 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) was similar to the high end of the range for the lichen critical load in chaparral and forests (Table 13.6). This grassland critical load is based on a site to the west of the Central Valley and downwind of the San Jose/San Francisco metropolitan area. The serpentine grassland critical load may be a reasonable estimate for California grasslands in more fertile soils of the Central Valley and other regions of California, 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). The critical load for NO_3^- leaching in chaparral catchments ($10 \text{ kg ha}^{-1} \text{ yr}^{-1}$) is about 60 percent of that for mixed-conifer forest ($17 \text{ kg ha}^{-1} \text{ yr}^{-1}$). The lower critical load in chaparral is believed to be due to the lower biological N demand and N retention capacity of chaparral catchments that are characterized by steep slopes and sandy soils. Another factor for the lower chaparral critical load may be the small size (4.3 ha) of the Chamise Creek catchment (Li et al. 2006) upon which the chaparral critical load of $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$ is based. Smaller catchments are often associated with lower N retention capacity (Meixner and Fenn 2004). Thus, it isn't clear if the critical load value for NO_3^- leaching from Chamise Creek is generally applicable to chaparral catchments.

For all vegetation types, catchment characteristics that increase the contact time of soil solution NO_3^- within the soil profile and with plant roots are expected to increase N uptake and increase the critical load. Stand

Table 13.6—Empirical critical loads of nutrient N for the Mediterranean California ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem	Critical load for N deposition ^a <i>kg N ha⁻¹ yr⁻¹</i>	Reliability	Response	Comments	Study
Coastal Sage Scrub	7.8-10	#	Exotic invasive grass cover, native forb richness, arbuscular mycorrhizal richness	Modeled and inferential N deposition estimates and published data for mycorrhizae, unpublished data for vegetation survey.	Allen unpublished ^b , Egerton-Warburton and Allen 2000, Tonnesen et al. 2007
Chaparral	3.1-14	#	NO ₃ leaching; changes in lichen communities	Critical load for NO ₃ leaching of 10 kg N ha ⁻¹ yr ⁻¹ is based on one year of throughfall data in Chamise Creek and an additional year of throughfall data from adjacent Ash Mountain, both in Sequoia National Park. Lichen critical load of 5.5 kg N ha ⁻¹ yr ⁻¹ is from modeled N deposition data and published data for lichens. Lower estimated value for the lichen critical load of 3.1 kg N ha ⁻¹ yr ⁻¹ is from application of a model developed in the Pacific NW including the effect of precipitation.	Fenn et al. 2003a; Fenn et al. 2003b; Fenn et al. 2010; Geiser et al. 2010; Jovan 2008; Jovan and McCune 2005; Meixner et al. 2006; Meixner and Fenn 2004; Riggan et al. 1985
Mixed-conifer forest	3-39	##	Lichen chemistry and community changes; NO ₃ leaching; soil acidification; reduced fine root biomass	The lowest critical load is based on lichen tissue chemistry above the clean site threshold. NO ₃ leaching and fine root biomass critical load is 17 kg N ha ⁻¹ yr ⁻¹ , and soil acidification critical load is 26 kg N ha ⁻¹ yr ⁻¹ .	Allen et al. 2007; Breiner et al. 2007; Fenn et al. 2008; Fenn et al. 2010; Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004
Serpentine grassland	6	##	Annual grass invasion, replacing native herbs	Critical load based on a local roadside gradient; Serpentine grassland site is actually west of the Central Valley.	Weiss 1999; Fenn et al. 2010

^aN deposition in the mixed-conifer sites is reported as throughfall. Critical loads for coastal sage scrub and for lichen communities in chaparral (5.5 kg N ha⁻¹ yr⁻¹) are based on CMAQ simulated N deposition.

^bSee footnote 15 on page 144

management is also expected to affect the critical load for a given site. For example, a decrease in the site N capital due to fire or stand thinning operation, followed by vigorous vegetation regrowth and increased N demand, could increase site N retention and thus lead to a higher critical load. The critical load for biological effects in coastal sage scrub is relatively low (10 to 11 kg ha⁻¹ yr⁻¹) and may be lower, considering the lack of low N deposition control sites in estimating the critical loads. A major factor contributing to the N sensitivity of coastal sage scrub vegetation is the fact that N accumulates to high concentrations in the surface soils during the long summer dry period and the entire rooting zone is probably only thoroughly leached of NO₃⁻ in unusually high rainfall years (Wood et al. 2006).

Mediterranean ecosystems exposed to chronic N deposition often cycle between periods of N accumulation and periods of N availability, mobilization, uptake, and loss. This latter period is presumably the season of greatest ecosystem sensitivity to the effects of excess N. Critical loads estimates are needed that protect ecosystems from detrimental effects during these periods of greatest sensitivity. The empirical critical loads in this study are based on the predominant ecological conditions, which include fire suppression, co-occurrence of O₃ and chronic N deposition, and recurring drought. Critical load, by definition, refers to the threshold deposition below which adverse biological effects are not observed. However, some critical loads in this chapter (and others) are tied to ecosystem processes or responses that don't always have a biological link within the terrestrial ecosystem that has yet been well established or defined (e.g., nitrate leaching).

13.6 Comparison to European Critical Loads

Few empirical N critical loads studies for European Mediterranean ecosystems have been published. Based on a European-wide modeling effort, Kuylensstierna et al. (1998) concluded that Mediterranean scrub has low to moderate sensitivity to N deposition, with a lower critical load of 15 kg N ha⁻¹ yr⁻¹. A relatively small area of the Mediterranean scrub exceeds this

level of deposition (Kuylensstierna et al. 1998). Lorenz et al. (2008) used the simple mass balance approach and reported low nutrient N critical load values for Spain, ranging from 3.5 to 10.5 kg ha⁻¹ yr⁻¹, or possibly even lower in some instances. These modeled critical load values appear to be lower than expected based on empirical studies (Fenn et al. 2008, Michopoulos et al. 2008, this chapter). Modeled deposition to coniferous forest for the year 2000 shows N deposition of 10 to 20 kg ha⁻¹ yr⁻¹ over most of Mediterranean Europe (Simpson et al. 2006), showing the potential for exceedance of the N critical load in many forested sites.

A critical load of 5 kg N ha⁻¹ yr⁻¹ as bulk deposition in forest clearings can be estimated for Spanish fir (*Abies pinsapo*) forests in southern Spain (Torres-Cañabate et al. 2008). Throughfall N deposition from an earlier study was reportedly 12 kg N ha⁻¹ yr⁻¹ in these forests (Torres-Cañabate et al. 2008). At the reported level of bulk deposition, N enrichment of soil and foliage were evident, along with increased potential net nitrification and emissions of N₂O from soil compared to a more N-limited site. However, bulk N deposition was higher at the N-limited site than the site showing symptoms of N saturation, making interpretation of these findings difficult (Torres-Cañabate et al. 2008). We estimate a tentative N critical load for incipient NO₃⁻ leaching at a beech forest in central eastern Greece of 13 kg N ha⁻¹ yr⁻¹, based on data reported by Michopoulos et al. (2008), but more data are needed to determine if the critical load is actually higher. Catchments in northern Italy along the Swiss border (Rogora 2007) are strongly N saturated (at level 2-3 of Stoddard's [1994] classification), but these are not typical Mediterranean ecosystems. A notable example of a Mediterranean forest where deposition exceeds the N critical load is an Aleppo pine site in Athens, Greece (Michopoulos et al. 2004). Because this site is presumably well above the critical load, with annual throughfall deposition as high as 38 kg N ha⁻¹ yr⁻¹, the critical load cannot be determined.

In summary, few European Mediterranean sites have been reported to be above the N critical loads based on empirical data. On the other hand, broad-scale models

of N deposition and nutrient N critical loads predict that critical loads exceedance is not uncommon in the European Mediterranean region (Lorenz et al. 2008, Simpson et al. 2006). Lorenz et al. (2008) calculated low critical load values in Spain because of low plant growth rates, low timber harvest, and low levels of N export in seepage water due to low precipitation, resulting in low net N export from the ecosystems. It was concluded that, in these cases, the critical load can be exceeded by relatively low N deposition. However, modeled deposition and critical loads need to be validated with empirical data, particularly considering the co-occurrence of elevated O₃ levels and the pronounced seasonality in precipitation and N deposition inputs and outputs in these unique Mediterranean ecosystems (Fenn et al. 2008). DeVries et al. (2007) also recommended that for these cases the empirical critical loads for N should be determined.

The N critical loads in European Mediterranean ecosystems appear to be generally similar to those in California, but the lack of reported empirical critical loads for Mediterranean Europe prevent any strong comparisons. It seems safe to assume that in both regions, lichens are the most sensitive terrestrial responders to N deposition, and are impacted in regions of sufficient exposure. Lichen responses to NH₃ have been reported from Italy and Portugal, but critical load estimates are not available due to lack of deposition data (Frati et al. 2008, Pinho et al. 2009). However, recent studies on the responses of epiphytic lichen communities to NH₃ exposure indicate similar dose responses in Europe and the Mediterranean California ecoregion. In an oak woodland in Portugal, also with a Mediterranean climate, the estimated critical level for lichen community diversity impacts was 1.4 to 1.7 µg m⁻³ (Pinho et al. 2009). The estimated critical level for epiphytic lichen community changes in mixed-conifer forests in the southern Sierra Nevada of California falls within this same range.²⁰ Recently a critical level of 1.0 µg m⁻³ as a long-term average concentration was proposed for NH₃ effects on epiphytic lichen

communities based on European studies (Cape et al. 2009, Sutton et al. 2009) and a critical level of 3.0 µg m⁻³ was proposed for effects on herbaceous plant communities (Cape et al. 2009). The California serpentine grassland results presented in this chapter are in general agreement with the herbaceous plant critical level for NH₃. Monthly average NH₃ concentrations were 0.3 to 0.7 µg m⁻³ at a site where impacts were minimal, compared to NH₃ concentrations of 1 to 3.5 µg m⁻³ at sites where plant communities were strongly impacted by invasive species.²¹

However, in regard to broader ecosystem effects from excess N, as suggested by Rodà et al. (2002) and in contrast to the conclusions of Lorenz et al. (2008) cited above, the N-limited state of some European Mediterranean ecosystems may be enhanced by the repeated nutrient losses from fire and biomass harvesting over the centuries. Under these N-demanding conditions, the critical loads for soil, vegetative, and hydrologic responses to N deposition may be higher than those reported for California. These effects of land-use history on the critical loads are expected to vary across the landscape. Information on critical loads for all vegetation types in Mediterranean ecosystems has been identified as a major research gap (Bobbink et al. 2003). Because of the dearth of critical load work in European Mediterranean ecosystems, the work summarized herein from California Mediterranean ecosystems may be useful to the European scientific community.

13.7 Future Research Directions and Gaps in Data

To better understand the effects of chronic N deposition in Mediterranean ecosystems, further research is needed on levels of N input and mechanisms and fluxes of N loss and storage, the effects of fire on N pools and processing, and the response of plant, lichen, and mycorrhizal communities to deposition. Gaseous N losses have not been well quantified and may be an important process by which a significant proportion of the excess N accumulation is reduced (Anderson and Poth 1989, Fenn

²⁰Bytnerowicz, A.; Jovan, S. Unpublished data on file with Andrzej Bytnerowicz, research ecologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

²¹Weiss, S.B.; Bytnerowicz, A. Unpublished data on file with Mark Fenn, research plant pathologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

et al. 1996, Fenn and Poth 2001). A large proportion of trace gas losses are expected to occur in the riparian and near-riparian zones, possibly as degassing of dissolved N_2O from groundwater-fed streams. Further streamwater measurements are needed across N deposition gradients using $\Delta^{17}\text{O}$ as a tracer for atmospheric NO_3^- (Michalski et al. 2004) to determine the threshold percent of exported NO_3^- as direct throughput of unassimilated atmospheric NO_3^- associated with N-saturated catchments. As stands with lower air pollution or N fertilization at realistic levels are studied, we may find that lower levels of N deposition also have effects on ecosystem dynamics. Research is needed on the best management practices for improving water quality in chaparral and mixed-conifer forest catchments. Questions remain regarding the level of N deposition reduction necessary to reverse the symptoms of saturation. It would be valuable to characterize the spatial patterns of N deposition throughout catchments, but this is difficult because of the steep terrain in many chaparral and forested catchments.

Research is needed on the effects of fire in Mediterranean ecosystems. Fire is a natural part of Mediterranean ecosystems, and its interactions with N deposition are complex. In coastal sage scrub, fire may interact with increased N deposition to promote the growth of exotic grass fuel and cause rapid degradation in native vegetation (Allen et al. 1998, Minnich and Dezzani 1998, Talluto and Suding 2008). In chaparral and mixed-conifer forests, fire in combination with decreased N deposition may help mitigate N saturation (Gimeno et al. 2009). Studies are needed to test the effectiveness of periodic fire as a management tool in N-saturated catchments, considering that 65 to 85 and 80 to 95 percent of site N capital in forest (Johnson et al. 2009) and chaparral (Rundel and Parsons 1980, Rundel and Vankat 1989) ecosystems is stored in the mineral soil, which is unimpacted by fire disturbance (Meixner et al. 2006). Recurring fire is a normal process in California chaparral and forest ecosystems and prescribed fire can be applied without causing significant alterations in nutrient cycling or plant nutrient status (Murphy et al. 2006).

Little is known about the effects of N deposition on plant biodiversity in chaparral and in the forest

understory, including the putative indirect effects on plant communities as a result of the impacts of N deposition on mycorrhizal communities. Nitrogen addition studies at appropriate doses are also needed to determine the N critical load for biodiversity effects in California grasslands. Additional analysis is needed to separate lichen responses due to NH_3 from those caused by other forms of N deposition in the oak woodlands, chaparral, and forest communities, and to account for the influence of precipitation on lichen responses to N deposition over the regional landscape. The original interpretation of lichen community work in the greater Central Valley was limited by available air pollution data. The simulated CMAQ deposition data presented herein has allowed for preliminary estimates of lichen-based critical loads in chaparral and oak woodlands. This should be complemented with empirical deposition data to better define the critical load for lichen community responses.

More work is needed to determine the critical load for acidity in chaparral ecosystems. Evidence strongly suggests that atmospheric deposition has acidified chaparral soils over the past several decades, but N deposition data are not available from enough sites to determine empirical relationships. Modeled estimates of the critical loads for acidity have not yet been made for chaparral ecosystems. Better definition is needed of the N input levels that contribute to decreases in forest sustainability by way of physiological perturbations, greater sensitivity to bark beetles, and increased drought stress and mortality (Grulke et al. 2009). Further comparisons of modeled and empirical critical loads are needed for California ecosystems and for Mediterranean ecosystems in general.

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