

Chapter 5

Effects and Empirical Critical Loads of Nitrogen for Ecoregions of the United States

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5.1 Introduction

5.1.1 *Effects of Nitrogen Deposition on Ecosystems*

Human activity in the last century has led to a significant increase in nitrogen (N) emissions and deposition (Galloway et al. 2004). Total N emissions in the United States have increased significantly since the 1950s (Galloway 1998, Galloway et al. 2003). As S deposition has declined in response to regulation, the rate of N deposition relative to S deposition has increased since the 1980s (Driscoll et al. 2001, 2003) followed by a general decrease in NO_x emissions from electric utilities since the early 2000s. More recently, the relative proportion of NH_x ($\text{NH}_4^+ + \text{NH}_3$) to NO_x ($\text{NO} + \text{NO}_2$) emissions has also increased for many areas of the United States (Kelly et al. 2005; Lehmann et al. 2005).

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Because of past, and, in some regions, continuing increases in emissions (Lehmann et al. 2005; Nilles and Conley 2001), N deposition has reached a level that has caused or is likely to cause alterations in many United States ecosystems. In some ecoregions, the impact of N deposition has been severe, altering N cycling and biodiversity. Indicators of altered N cycling include increased N mineralization, nitrification, and nitrate (NO_3^-) leaching rates, as well as elevated plant tissue N concentration. The eventual outcome of increases in these processes can be N saturation, the series of ecosystem changes that occur as available N exceeds plant and microbial demand (Aber et al. 1989, 1998).

As N availability increases, there are progressive changes in biotic community structure and composition, including changes in diatom, lichen, mycorrhizal fungal and terrestrial plant communities. For example, in the Mediterranean California ecoregion, native plant species in some ecosystems have been replaced by invasive species that are more productive under elevated N deposition (Fenn et al. 2010;

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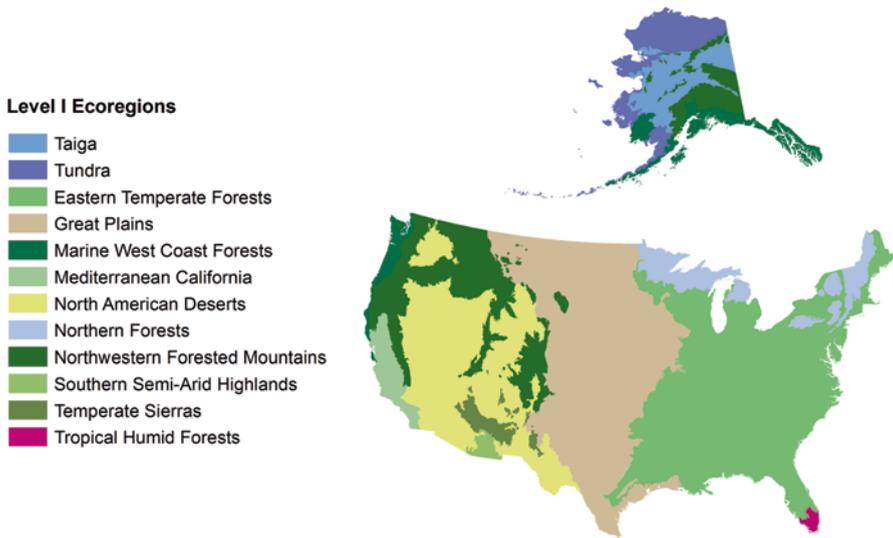


Fig. 5.1 Level I ecological regions in the United States. (Commission for Environmental Cooperation 1997)

Rao and Allen 2010; Rao et al. 2010; Weiss 1999; Yoshida and Allen 2004). Such shifts in plant community composition and species richness can lead to overall losses in biodiversity and further impair particular threatened or endangered species (Stevens et al. 2004), as has occurred for the checkerspot butterfly (Weiss 1999).

5.1.2 Approach for Determining Empirical Critical Loads of Nitrogen

Recently, Pardo et al. (2011a–d) synthesized research relating atmospheric N deposition to effects on terrestrial and freshwater ecosystems in the United States and quantified empirical critical loads of atmospheric N deposition, with one chapter devoted to each of 12 major ecoregions. This chapter summarizes those findings and includes a brief discussion of the approach used to set critical N loads.

For this synthesis, we reviewed studies of responses to N inputs for U.S. ecoregions as defined by the Commission for Environmental Cooperation (CEC) Level I ecoregions map for North America (CEC 1997; Fig. 5.1). We estimated critical loads based on data from >3200 sites (Fig. 5.2). We identified the receptor of concern (organism or ecosystem compartment), the response of concern, the critical threshold value for that response, and the criteria for setting the critical load and extrapolating the critical load to other sites or regions. These methods are described in detail in Pardo et al. (2011a, b, d).

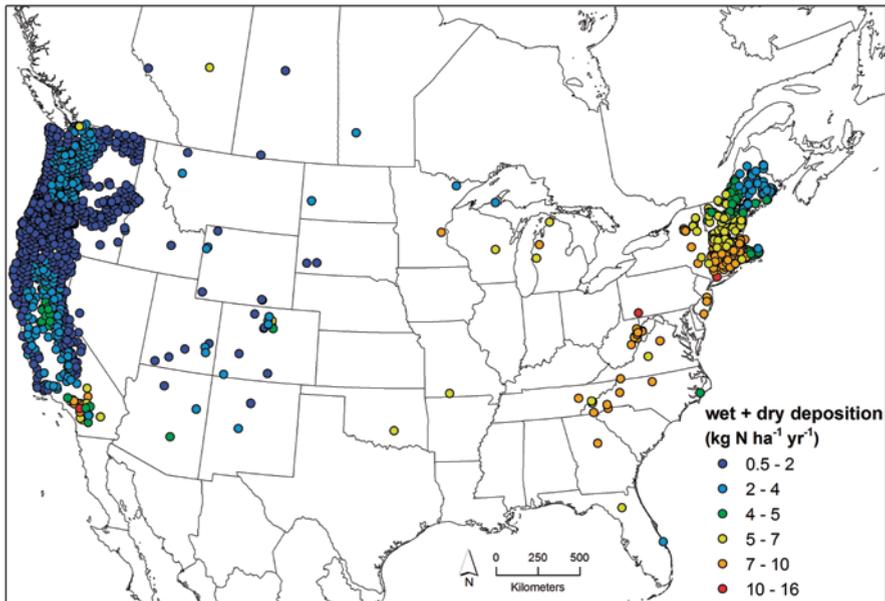


Fig. 5.2 Locations of > 3200 sites in the United States with modelled N deposition for which ecological responses are reported

The receptors evaluated included freshwater diatoms, mycorrhizal fungi, lichenized fungi (henceforth lichens), bryophytes, herbaceous plants, shrubs, and trees. Ecosystem impacts included: (1) biogeochemical responses and (2) individual species, population, and community responses. We considered N addition (fertilization) experiments, N deposition gradient studies and long-term monitoring studies in order to evaluate ecosystem response to N deposition inputs. Nitrogen deposition at sites included in this analysis (Weathers and Lynch 2011) was either based on the deposition reported in the publication or, when that was not available, we used modelled deposition quantified by the Community Multiscale Air Quality (CMAQ) model v.4.3 simulations of wet + dry deposition of oxidized (NO_x) and reduced (NH_x) N species (Fig. 5.2). Hereafter, this model is referred to as CMAQ 2001, as it uses 2001 reported data (Byun and Schere 2006; Byun and Ching 1999). In some areas of elevated N deposition, CMAQ at this grid scale (36 km) likely underestimates total N deposition. This is the case, for example, over much of California (Fenn et al. 2010). For more detail on deposition, see Weathers and Lynch (2011). We afforded greater weight to long-term fertilization studies (5–10 years) than to short-term studies. Single-dose forest fertilization studies exceeding 50 kg N ha^{-1} were generally not considered, but lower dose short-term studies were considered when other observations were limited.

We rarely had data to distinguish biotic or ecosystem response to reduced forms versus oxidized forms of N. There is some evidence that for some species, reduced forms of N may have more substantial impacts than oxidized forms (Bobbink et al. 2003; Cape et al. 2009; Kleijn et al. 2008; Sutton et al. 2009). Differences in uptake rates and preference for NH_4^+ versus NO_3^- across different plant taxa (Falkengren-Grerup 1995; McKane et al. 2002; Miller and Bowman 2002; Nordin et al. 2006) lead to differences in sensitivity to NH_x (Krupa 2003) and NO_y . However, not all species are more sensitive to NH_x than NO_y (Jovan et al. 2012); these responses vary by species and functional type. Some species are more sensitive to increases in NO_y , as was demonstrated for boreal forests (Nordin et al. 2006).

In general, we determined the critical load based on the observed response pattern to N inputs. In some cases, there was a clear dose-response relationship where the response changed above a certain threshold. In other cases, when response to increasing N was more linear, we estimated the “pristine” state of N deposition and the deposition that corresponded to a departure from that state. The criteria for setting critical loads are discussed in detail in Pardo et al. (2011a, b, d).

5.1.3 Contents of this Chapter

In this chapter we synthesize empirical critical loads of N reported for all the ecoregions of the United States, compare critical loads by life form or ecosystem compartment across all ecoregions, discuss the abiotic and biotic factors that affect the critical loads, present the significance of these findings and, finally, compare critical loads in the United States to those for similar ecoregions/ecosystems in Europe. For each receptor, we present maps of critical loads by ecoregion.

The range of critical loads of nutrient N reported for the United States ecoregions, inland surface waters, and freshwater wetlands is 1–39 kg N ha⁻¹yr⁻¹ (Table 5.1). This broad range spans the range of N deposition observed over most of the country (see Weathers and Lynch 2011). The number of locations for which ecosystem response data were available (Fig. 5.2) for an ecoregion is variable, which impacts the level of certainty of the empirical critical loads estimates.

5.2 Mycorrhizal Fungi

Mycorrhizal fungi reside at the interface between host plants and soils, exchanging soil resources, especially nutrients, with host plants in exchange for photosynthates (carbon compound). Due to this important and unique ecological niche, mycorrhizal fungi are at particular risk due to changes in either the soil environment or host carbon allocation.

Table 5.1 Summary of critical loads of nutrient N for United States ecoregions including their reliability

Ecoregion	Ecosystem component	CL for N deposition kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Tundra	Prostrate dwarf shrubs	1–3	##	Changes in CO ₂ exchange, cover, foliar N, and community composition of vascular plants	N addition study, Greenland high arctic, P enhanced N effects	(Arens et al. 2008) ^a
Tundra	Lichens	1–3	(#)	Changes in lichen pigment production and ultrastructure, changes in lichen and bryophyte cover	N addition studies, high and low arctic, P enhanced or moderated N effects	(Hyvärinen et al. 2003) ^b ; (Makkonen et al. 2007) ^b ; (Arens et al. 2008) ^a ,
Taiga	Lichen, moss, and algae in forests and woodlands	1–3	#	Changes in alga, bryophyte, and lichen community composition, cover, tissue N or growth rates		(Poikolainen et al. 1998) ^b ; (Strengbom et al. 2003) ^d ; (Vitt et al. 2003) ^c ; (Berryman et al. 2004) ^c ; (Moore et al. 2004) ^c ; (Berryman and Straker 2008) ^e ; (Geiser et al. 2010)
Taiga	Spruce forests	5–7	(#)	Change in ectomycorrhizal fungal community structure	Expert judgment, extrapolated from Marine West coast spruce and northern spruce-fir forest	(Lilleskov 1999); (Lilleskov et al. 2001, 2002, 2008)
Taiga	Shrublands	6	##	Change in shrub and grass cover, increased parasitism of shrubs	Long term, low N addition study: shrub cover decreased, grass cover increased	(Strengbom et al. 2003) ^d ; (Nordlin et al. 2005) ^d
Northern Forests	Hardwood and Coniferous Forests	>3	#	Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood		(Thomas et al. 2010)

Table 5.1 (continued)

Ecoregion	Ecosystem component	CL for N deposition kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Northern Forests	Lichens	4-6	(#)	Epiphytic lichen community change	Loss of oligotrophic species. Synergistic and/or confounding effects of acidic deposition not considered; assumes response threshold similar to Marine West Coast Forest	(Geiser et al. 2010)
Northern Forests	Ectomycorrhizal fungi	5-7	#	Change in fungal community structure		(Lilleskov et al. 2008)
Northern Forests	Herbaceous cover species	>7 and <21	#	Loss of prominent species	Response observed in low-level fertilization experiment	(Hurd et al. 1998)
Northern Forests	Hardwood and Coniferous Forests	8	##	Increased surface water NO ₃ leaching		(Aber et al. 2003)
Northern Forests	Old-growth montane red spruce	>10 and <26	#	Decreased growth and/or induced mortality	Response observed in low-level fertilization experiment	(McNulty et al. 2005)
Northern Forests	Arbuscular mycorrhizal fungi	<12	(#)	Biomass decline and community composition change		(Van Diepen et al. 2007); (Van Diepen 2008)
Northwest Forested Mountains	Alpine lakes	1.5	##	Changes in diatom assemblages	As wet deposition only	(Baron 2006)
Northwest Forested Mountains	Lichens	1.2-3.7	(#)	Epiphytic lichen community change in mixed-conifer forests, Alaska	Application of western Oregon and Washington model	(Geiser et al. 2010)

Table 5.1 (continued)

Ecoregion	Ecosystem component	CL for N deposition $\text{kg N ha}^{-1}\text{yr}^{-1}$	Reliability	Response	Comments	Study
Northwest Forested Mountains	Lichens	2.5–7.1	##	Epiphytic lichen community change, thallus N enrichment in mixed-conifer forests, non-Alaska		(Fenn et al. 2008); (Geiser et al. 2010)
Northwest Forested Mountains	Sub-alpine forest	4	##	Increase in organic horizon N, foliar N, potential net N mineralization, and soil solution N; initial increases in N leaching below the organic layer		(Baron et al. 1994); (Rueth and Baron 2002)
Northwest Forested Mountains	Alpine lakes	4.0	#	Episodic freshwater acidification		(Williams and Tonnesen 2000)
Northwest Forested Mountains	Alpine grassland	4–10	##	Changes in plant species composition		(Bowman et al. 2006)
Northwest Forested Mountains	Ectomycorrhizal fungi	5–10	(#)	Changes in ectomycorrhizal fungal community structure in white, black, and Engelmann spruce forests	Expert judgment, extrapolated from Marine West Coast spruce and northern spruce-fir forest	(Lilleskov 1999); (Lilleskov et al. 2001, 2002, 2008)
Northwest Forested Mountains	Mixed conifer forest	17	## #	NO_3^- leaching reduced fine root biomass		(Fenn et al. 2008)
Marine West Coast Forests	Western OR and WA forests	2.7–9.2	##	Epiphytic lichen community change	Loss of oligotrophic species, enhancement of eutrophic species. CL increases with regional range in mean annual precipitation from 45–450 cm	(Geiser et al. 2010)

Table 5.1 (continued)

Ecoregion	Ecosystem component	CL for N deposition kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Marine West Coast Forests	SE Alaska forests	5	(#)	Fungal community change; declines in ectomycorrhizal fungal diversity		(Whytemare et al. 1997); (Lilleskov 1999), (Lilleskov et al. 2001, 2002)
Eastern Temperate Forest	Eastern Hardwood Forest	>3	#	Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood		(Thomas et al. 2010)
Eastern Temperate Forest	Lichens	4–8	(#)	Epiphytic lichen community change	Loss of oligotrophic species. Synergistic/ confounding effects of acidic deposition not considered; based on application of model and estimated response threshold	(Geiser et al. 2010)
Eastern Temperate Forest	Southeast Coastal Plain	5–10	(#)	Ectomycorrhizal fungi community change		(Lilleskov et al. 2001, 2002, 2008); (Dighton et al. 2004)
Eastern Temperate Forest	Eastern Hardwood Forests	8	##	Increased surface water NO ₃ leaching		(Aber et al. 2003)
Eastern Temperate Forest	Michigan deposition gradient	<12	(#)	AMF biomass decline and community composition change		(Van Diepen et al. 2007); (Van Diepen 2008)
Eastern Temperate Forest	Herbaceous species	<17.5	(#)	Increases in nitrophilic species, declines in species-rich genera (e.g., <i>Viola</i>)		(Gilliam 2006, 2007); (Gilliam et al. 2006)

Table 5.1 (continued)

Ecoregion	Ecosystem component	CL for N deposition kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Great Plains	Tall-grass prairie	5–15	#	Biogeochemical N cycling, plant and insect community shifts		(Tilman 1987, 1993); (Wedin and Tilman 1996); (Clark and Tilman 2008); (Clark et al. 2009)
Great Plains	Mixed-grass prairie	10–25	#	Soil NO ₃ ⁻ pools, leaching, plant community shifts		(Clark et al. 2003, 2005); (Jorgensen et al. 2005)
Great Plains	Short-grass prairie	10–25	(#)		Inferred from mixed grass	(Epstein et al. 2001); (Barret and Burke 2002)
Great Plains	Mycorrhizal fungi	12	(#)	Decline in arbuscular mycorrhizal fungal activity		Egerton-Warburton, unpub. data
North American Desert	Lichens	3	(#)	Lichen community shifts, thal-lus N concentration	Uncertainty regarding modelled deposition estimates	(Porter 2007); (Geiser et al. 2008)
North American Desert	Shrubland, woodland, desert grassland	3–8.4	#	Vegetation response, vascular plant community change		(Inouye 2006); (Baez et al. 2007); (Allen et al. 2009); (Rao et al. 2010)
Mediterranean California	Coastal Sage Scrub	7.8–10	#	Invasive grass cover, native forb richness, arbuscular mycorrhizal fungi richness	Modelled and inferential N deposition estimates and published data for mycorrhizae, unpublished data for vegetation survey	¹ Allen unpublished data; (Egerton-Warburton and Allen 2000); (Tonnesen et al. 2007); (Fenn et al. 2010)
Mediterranean California	Chaparral; Lichens	3–6	#	Epiphytic lichen community change	Lichen critical loadis from modelled N deposition data and published data for lichens	(Jovan and McCune 2005); (Jovan 2008); (Fenn et al. 2010); (Geiser et al. 2010)

Table 5.1 (continued)

Ecoregion	Ecosystem component	CL for N deposition kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Mediterranean California	Chaparral, Oak Woodlands, Central Valley	10–14	#	NO ₃ ⁻ leaching; stimulated N cycling	Critical load for NO ₃ ⁻ leaching of 10 kg N ha ⁻¹ yr ⁻¹ is based on 1 year of throughfall data in Chamise Creek and an additional year of throughfall data from adjacent Ash Mountain, both in Sequoia National Park	(Fenn and Poth 1999); (Fenn et al. 2003a, 2003b, 2003c, 2009, 2011); (Meixner and Fenn 2004)
Mediterranean California	Mixed conifer forest; Lichens	3.1–5.2	##	Lichen chemistry and community changes	The lowest critical load is based on lichen tissue chemistry above the clean site threshold	(Fenn et al. 2008, 2010)
Mediterranean California	Mixed conifer forest	17	#	Reduced fine root biomass		(Grulke et al. 1998); (Fenn et al. 2008, 2010)
Mediterranean California	Mixed conifer forest	17–25.9	#	NO ₃ ⁻ leaching; soil acidification		(Breiner et al. 2007); (Fenn et al. 2008, 2010)
Mediterranean California	Mixed conifer forest	24–39	(#)	Understory biodiversity; forest sustainability	N deposition from Fenn et al. (2008)	(Grulke et al. 1998, 2009); (Grulke and Balduman 1999); (Jones et al. 2004); (Allen et al. 2007)
Mediterranean California	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)

Table 5.1 (continued)

Ecoregion	Ecosystem component	CL for N deposition kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Temperate Sierras	Lichens	4–7	(#)	Epiphytic lichen community change	Increase in proportion of eutrophic species. Estimated from Marine West Coast Forests model, response threshold allows ~60% eutrophs due to dry, hot climate, hardwood influence	(Geiser et al. 2010)
Temperate Sierras	<i>Pinus</i> forest	15	#	Elevated NO ₃ ⁻ in stream and spring waters	Data are from <i>Pinus hartwegii</i> sites in the Desierto de los Leones National Park and Ajusco, Mexico	(Fenn et al. 1999, 2002); (Fenn and Geiser 2011)
Tropical and Subtropical Humid Forests	N-rich forests	<5–10	(#)	NO ₃ ⁻ leaching, N trace gas emissions	CL for N-rich forests should be lower than for N-poor forests based on possibility of N losses	ND
Tropical and Subtropical Humid Forests	N-poor forests	5–10	(#)	Changes in community composition; NO ₃ ⁻ leaching, N trace gas emissions	CL for N-poor forests based on estimates for Southeastern Coastal Plain forests	ND
Wetlands	Freshwater wetlands	2.7–13	#	Peat accumulation and NPP change	CL for wetlands in the northeastern U.S. and southeastern Canada	(Rochefort et al. 1990) ^c ; (Aldous 2002) ^c ; (Vitt et al. 2003) ^c ; (Moore et al. 2004) ^c
Wetlands	Freshwater wetlands	6.8–14	(#)	Sarracenia purpurea community change	CL based on northeastern populations	(Grotelli and Ellison 2002, 2006)

Table 5.1 (continued)

Ecoregion	Ecosystem component	CL for N deposition kg N ha ⁻¹ yr ⁻¹	Reliability	Response	Comments	Study
Wetlands	Intertidal wetlands	50–100	##	Loss of eelgrass		(Latimer and Rego 2010)
Wetlands	Intertidal salt marshes	63–400	(#)	Changes in salt marsh community structure, microbial activity and biogeochemistry		(Wigand et al. 2003); (Cafrey et al. 2007)
Aquatic	Western Lakes	2	##	Freshwater eutrophication		(Baron 2006)
Aquatic	Eastern Lakes	8	#	NO ₃ ⁻ leaching		(Aber et al. 2003)

reliable, # fairly reliable, (#) expert judgment

^a based on data from Greenland

^b based on data from Finland

^c based on data from Canada

^d based on data from Sweden

¹ Allen, E.B. unpublished data. Professor and Natural Resource Extension Specialist, Department of Botany and Plant Sciences and Center for Conservation Biology, University of California, Riverside, CA, 92521.

5.2.1 *Effects of Nitrogen Deposition*

Nitrogen deposition adversely affects mycorrhizal fungi (1) by causing decreased belowground C allocation by hosts and increased N uptake and associated metabolic costs (Wallander 1995) and (2) via soil chemical changes associated with eutrophication and acidification. There are two major groups of mycorrhizal fungi that are evolutionarily and ecologically distinct: arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF). Under sufficiently high N inputs, the progressive effect of elevated N is an early decline of sporocarp (reproductive structure) production for EMF and spore production for AMF, and subsequent decline in biological diversity and loss of taxa adapted to N-poor environments or sensitive to acidification (Lilleskov 2005). Sporocarp and spore production appears to be especially sensitive to N deposition, often declining before the communities on root tips have been substantially altered, presumably because sporocarps and spores are at the end of the carbon flux pathway from hosts.

Of the two plant-fungal symbioses examined here, mycorrhizal fungi appear to be less sensitive to N deposition than lichens, presumably because the soil environment buffers these soil fungi from some of the immediate impacts of N deposition to which lichens are directly exposed. Lichens have an advantage as indicators when compared with mycorrhizal fungi because they can be relatively easily inventoried. However, the critical role of mycorrhizal fungi as (i) root symbionts, central to plant nutrition and belowground production, (ii) repositories of a large part of the eukaryote diversity in forests, (iii) major components of food webs, and (iv) non-timber forest products of high economic value (edible sporocarps or mushrooms) (Amaranthus 1998), provides sufficient impetus to improve our understanding of their response to N deposition.

5.2.2 *Critical Loads of Nitrogen*

We reviewed empirical studies on mycorrhizal fungal response to N inputs to determine empirical critical loads for different ecoregions the United States (Table 5.1; Fig. 5.3). Nitrogen deposition sufficient to elevate inorganic N, especially NO_3^- , availability in soils can have measurable effects on mycorrhizal fungi. The data for EMF indicate that N deposition to N-limited conifer forests in the range of 5–10 kg $\text{ha}^{-1}\text{yr}^{-1}$ can significantly alter community structure and composition and decrease species richness (Dighton et al. 2004; Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008). Similarly, the data for AMF suggest that N deposition levels of 7.8–12 kg $\text{ha}^{-1}\text{yr}^{-1}$ can lead to community changes, declines in spore abundance and root colonization, and changes in community function. This range is based on re-analysis of data from Egerton-Warburton et al. (2001) combined with N deposition data, decreases in fungal abundance (Van Diepen et al. 2007, Van Diepen 2008), and

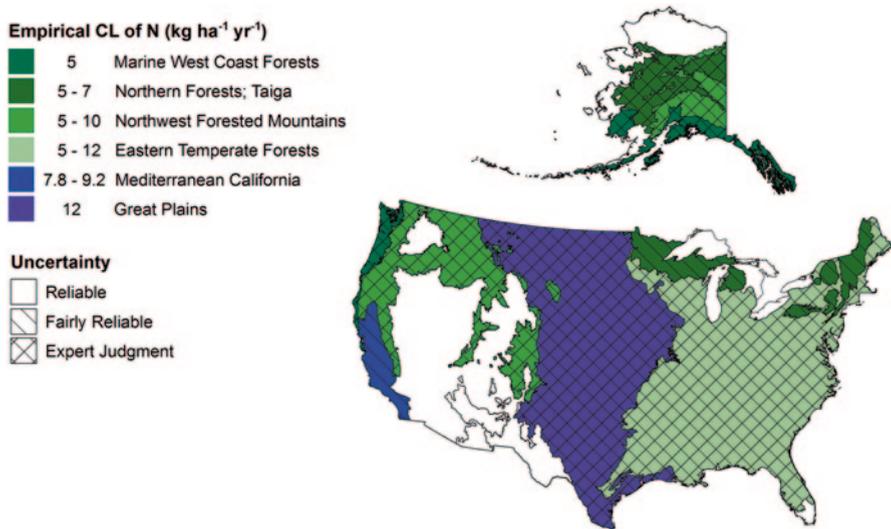


Fig. 5.3 Map of critical loads for mycorrhizal fungi by ecoregion in the United States (The *hatch marks* indicate increasing level of uncertainty: *no hatch marks* for the most certain “reliable” category, *single hatching* for the “fairly reliable” category, and *double hatching* for the “expert judgment” category. The colour sequence moves from red toward *blue* and *violet* as the critical load increases. As the range of the critical load gets broader, the saturation of the colour decreases)

declines in fungal activity². The actual threshold for N effects on AMF could be even lower, because high background deposition precludes consideration of sites receiving deposition at or near pre-industrial levels. Therefore, the provisional expert judgment is that critical loads for mycorrhizal diversity for sensitive ecosystem types are 5–10 $\text{kg ha}^{-1}\text{yr}^{-1}$. The uncertainty of this estimate is high, because few studies have been conducted at low N deposition to further refine the critical load. Variation across ecoregions is associated with differences in EMF and AMF responses. Critical load values are lower in Marine West Coast Forests, Northern Forests, Taiga, and Northwestern Forested Mountains, with EMF as receptors. Eastern Forests, which include both EMF and AMF as receptors, have the greatest range in critical loads values. Mediterranean California and the Great Plains, with only values for AMF reported, have the highest critical loads.

² Egerton-Warburton, L.M. Unpublished data. Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL, 60022.

5.3 Lichens and Bryophytes

Lichens and bryophytes make substantial contributions to biodiversity. About 4100 lichens and 2300 bryophytes are known from North America north of Mexico—approximately one fourth of the number of vascular plant species (about 26,600 species; USDA NRCS 2009).

5.3.1 *Effects of Nitrogen Deposition*

Lichens and bryophytes are among the most sensitive bioindicators of N in terrestrial ecosystems (Blett et al. 2003; Bobbink et al. 2003; Fenn et al. 2003b, 2010; Glavich and Geiser 2008). Unlike vascular plants, lichens and bryophytes lack specialized tissues to mediate the entry or loss of water and gases (e.g., waxy epidermis, guard cells, root steele). Thus, they rapidly hydrate and absorb gases, water, and dissolved nutrients during high humidity or precipitation events. However, they dehydrate to a metabolically inactive state quickly as well, making them slow growing and vulnerable to contaminant accumulation. Consequently, the implementation of lichen or bryophyte-derived critical loads may prevent undesired impacts, such as declines in biological diversity, to much of the broader forest ecosystem (McCune et al. 2007).

Species of epiphytic lichens in wet and mesic forests that are most sensitive to N (i.e., the large pendant and foliose species) play important ecological roles that are not duplicated by the nitrophytic (i.e., N tolerant) species that may replace them. Dominant regional oligotrophs (e.g. *Alectoria*, *Bryoria*, *Lobaria*, *Ramalina*, *Usnea*) comprise the bulk of lichen biomass in old-growth forests, contribute to nutrient cycling through N₂ fixation, and are used for nesting material, essential winter forage for rodents and ungulates, and invertebrate habitat (McCune and Geiser 2009). Storage of water and atmospheric nutrients by these lichen genera and epiphytic bryophytes moderates humidity and provides a slow release system of essential plant nutrients to the soil (Boonpragob et al. 1989; Cornelissen et al. 2007; Knops et al. 1991; Pypker 2004). In the tundra, lichens and bryophytes represent a significant portion of the biomass, and reindeer lichens are a vital link in the short arctic food chain (Kytöviita and Crittenden 2007). Mosses comprise the bulk of the biomass of the extensive boreal peatlands. In the desert, together with other microbiota, lichens and bryophytes form cryptogamic mats important to soil stabilization and fertility.

5.3.2 *Critical Loads of Nitrogen*

The critical loads estimated (Pardo et al. 2011c) for lichens range from 1–9 kg N ha⁻¹yr⁻¹ (Fig. 5.4; Table 5.1). The certainty associated with these estimates for li-

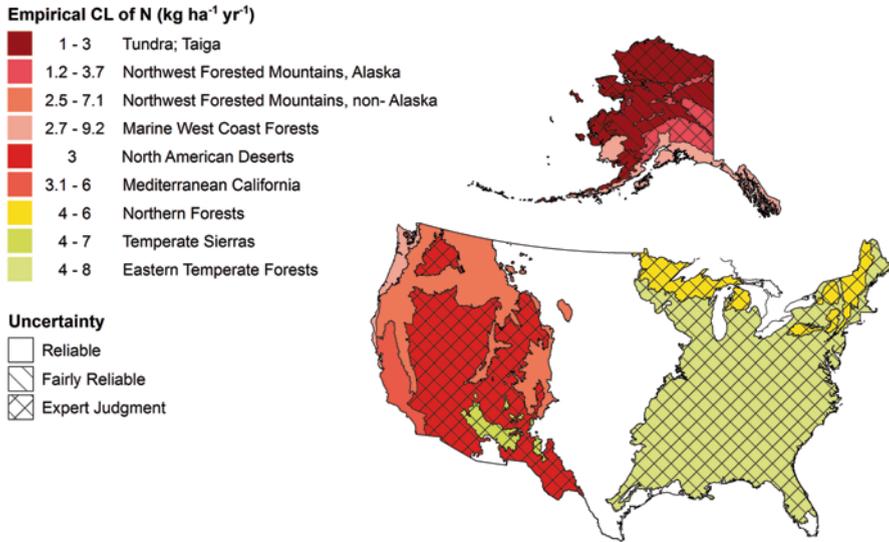


Fig. 5.4 Map of critical loads for lichens by ecoregion in the United States (see Fig. 5.3 for legend explanations)

lichens varies considerably by ecoregion. This is partially because of differences in sampling scheme and intensity. For example, in the Pacific Northwest lichen communities were assessed intensively across wide environmental gradients spanning low to high N deposition on a fine grid over time, yielding highly reliable critical N load estimates (Geiser and Neitlich 2007; Jovan 2008), whereas assessments in the eastern United States are more problematic due to historical and contemporary S and N deposition. It is more difficult to determine the critical load where historical information necessary to identify a “pristine” or “clean” state is lacking, and the resulting confidence associated with the critical load is low.

The intensive studies in the Pacific Northwest facilitated the development of simple regressions to relate N deposition with shifts in community composition (Geiser and Neitlich 2007; Geiser et al. 2010; Jovan 2008) and thus to set critical loads. If such simple models could be tested and confirmed in other regions of the country, the confidence in the critical loads in those regions would improve.

The variation in critical loads for lichens across ecoregions (Fig. 5.4) is among others due to differences in ecosystem type, pre-existing lichen communities, and background N deposition. Marine West Coast Forests, with its broad range in environmental gradients, has the greatest range in critical loads. The low end of the critical load range in eastern ecoregions is higher than the low end of the critical load range in western ecoregions, likely as a result of higher historical S and N deposition in the eastern United States, which makes it difficult to establish critical loads for sensitive species.

5.4 Herbaceous Plants and Shrubs

Herbaceous species and shrubs are found in grasslands, shrublands, forests, deserts, and wetlands and comprise the majority of the roughly 26,600 vascular plant species found in North America north of Mexico (USDA NRCS 2009). Herbaceous plants play an important role in those ecosystems in which they are the dominant primary producers (e.g., grasslands, shrublands). In forests, however, the role of the herbaceous community in ecosystem function also has a significance disproportionate to its low relative biomass. For example, although they represent only ~0.2% of standing above-ground biomass, herbaceous understory species produce >15% of forest litter biomass and comprise up to 90% of forest plant biodiversity, including endangered or threatened species (Gilliam 2007).

5.4.1 *Effects of Nitrogen Deposition*

Herbaceous plants and some shrubs appear intermediate between cryptogam and tree species in their sensitivity to N deposition, due to specialized tissues that mediate the entry or loss of water and gases compared with cryptogams, and rapid growth rates, shallow rooting systems, and often shorter lifespan compared with trees. Thus, herbaceous species in a forest understory will likely respond more rapidly to changes in N deposition and to a greater degree than the trees with which they coexist. Herbaceous plants in alpine or tundra environments will respond later and to a lesser degree than the cryptogams with which they coexist.

5.4.2 *Critical Loads of Nitrogen*

The range of critical loads of N for herbaceous plants and shrubs across all ecoregions is 3–33 kg N ha⁻¹yr⁻¹ (Fig. 5.5; Table 5.1). Although this range is broader than those for lichens or mycorrhizal fungi, many of the critical loads for herbaceous plants fall into the range of 5–15 kg N ha⁻¹yr⁻¹. The uncertainty of these estimates is moderate. The shorter lifespan of some herbaceous plants can result in a more rapid response to N addition. This is especially relevant for annuals or perennials with little N storage. In grasslands, for example, elevated N deposition often leads to a rapid (1–10 years) increase in herbaceous production and a shift in biomass allocation towards more above-ground tissue. This often decreases light levels at ground surface and decreases the numbers of plant species, primarily of perennials, legumes, and natives (Clark and Tilman 2008; Suding et al. 2004; Tilman 1993).

As a result of this relatively rapid response, experimental studies of moderate to long duration (3–10 years) allow determination of the critical load with reasonable certainty. Longer studies (>10 years) would decrease the uncertainty further. In some cases, it can be difficult to determine whether the condition in reference plots or at the low end of a deposition gradient represents a “pristine” condition or

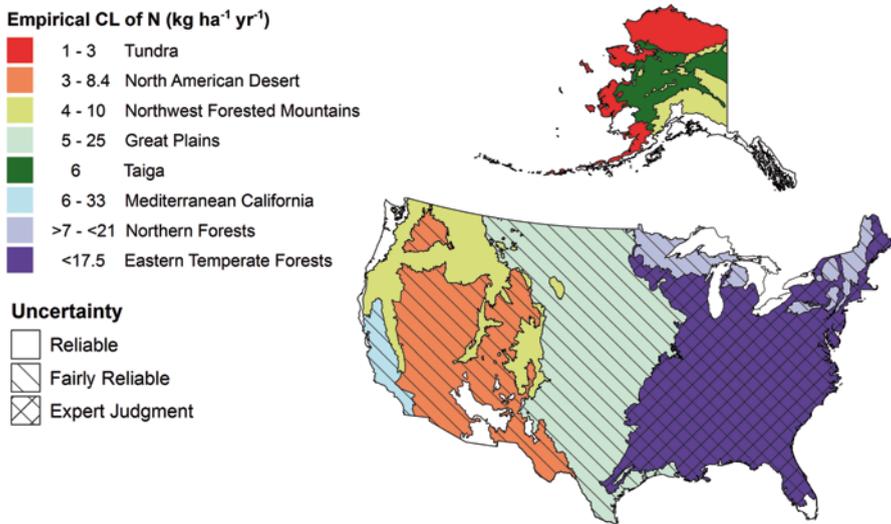


Fig. 5.5 Map of critical loads for herbaceous plants and shrubs by ecoregion in the United States (see Fig. 5.3 for legend explanations)

whether a site has already been altered by N deposition prior to or at the time of the study. For example, the Watershed Acidification Study at Fernow Experimental Forest, West Virginia, added $35 \text{ kg N ha}^{-1}\text{yr}^{-1}$ via aerial application in addition to ambient deposition of $15\text{--}20 \text{ kg N ha}^{-1}\text{yr}^{-1}$, which has led to changes in understory species composition (Adams et al. 2006). Recently, similar changes in understory species composition have occurred on the adjacent reference watershed receiving only ambient atmospheric deposition³ (Gilliam et al. 1996) suggesting that the deposition to the reference watershed currently exceeds the critical load. Where deposition rates exceed the critical load, measurement of the rate of change of an ecological metric (e.g. plant abundance, diversity, or community composition) over a range of N inputs provides an estimate of the N level at which increased ecological change occurs (Bowman et al. 2006), but it is difficult to determine the critical load.

The large variation across ecoregions for herbaceous critical loads (Fig. 5.5) is caused, in part, by the differences in receptor species and ecosystems, the paucity of data in some ecoregions and historic N status. Where few studies are available, the range reported for the critical load is broad and is considered less reliable. Additional studies could narrow the range of the critical load and increase the reliability. N-poor sites and sites with relatively low productivity (e.g., Tundra, North American Deserts) have lower critical loads for herbaceous species than sites with more fertile soil and higher productivity (e.g., Great Plains). High levels of historical N deposition and lack of low-level N fertilization experiments mean that the critical loads for some ecoregions may be lower than currently reported.

³ Gilliam, F.S. Unpublished data. Professor, Department of Biological Sciences, Marshall University, Huntington, WV 25755–2510.

5.5 Trees/Forest Ecosystems

In this section we discuss the responses of trees and the overall biogeochemical responses of forest ecosystems to N inputs, excluding the specific responses of mycorrhizal fungi, lichens, or understory herbaceous plants. Forest ecosystems represent about a third of landcover in the United States (USFS 2001) and are significant in Northern, Eastern, Tropical Wet, and Marine West Coast Forests, Northwestern Forest Mountains, and Mediterranean California ecoregions.

5.5.1 *Effects of Nitrogen Deposition*

In northeastern forests, gradient studies demonstrate that N deposition enhances growth in some fast-growing tree species, including many hardwoods with AMF associations, whereas it slows growth in some EMF species (red spruce, red pine), and has no detectable effect on still other species (Thomas et al. 2010). Similarly, N deposition enhances survivorship in a few species capable of forming AMF associations (black cherry, red maple, paper birch) and decreases survivorship in others, all ectomycorrhizal (Thomas et al. 2010). Survivorship under chronic N deposition, and possibly other co-occurring pollutants such as ozone, is often dependent on interactions with other stressors such as pests, pathogens, climate change, or drought (Grulke et al. 2009; McNulty and Boggs 2010). Over the long-term, these differential effects of N deposition on tree growth and survivorship are likely to shift species composition, possibly to more nitrophilic species, similar to patterns seen for organisms with shorter lifespans.

We have few data that show a major structural or functional shift in forest ecosystems, due to the long response times of trees and forest soils to changes in N inputs and N availability. This is caused by the relatively large pools of organic N in the forest floor, mineral soil, tree biomass, and detritus. Because of the long lag-time in response to N treatments, it can be difficult to determine the actual critical load of N for forest ecosystems based on short-term fertilization studies. If a response is observed over a relatively short period of time (i.e. years), it is nearly certain that the critical load is below the total N input at the treatment site and it can be difficult to further constrain the critical load. It is expected that the more complex and interconnected processes in forests will result in a higher critical load than other ecosystem types, in part because large N storage pools give forest ecosystems a greater capacity to buffer N inputs.

5.5.2 *Critical Loads of Nitrogen*

The range of critical loads reported for forest ecosystems is 4–39 kg N ha⁻¹yr⁻¹ (Fig. 5.6; Table 5.1). The threshold N deposition value which caused increased NO₃⁻ leaching from forest ecosystems into surface water was 8–17 kg N ha⁻¹yr⁻¹;

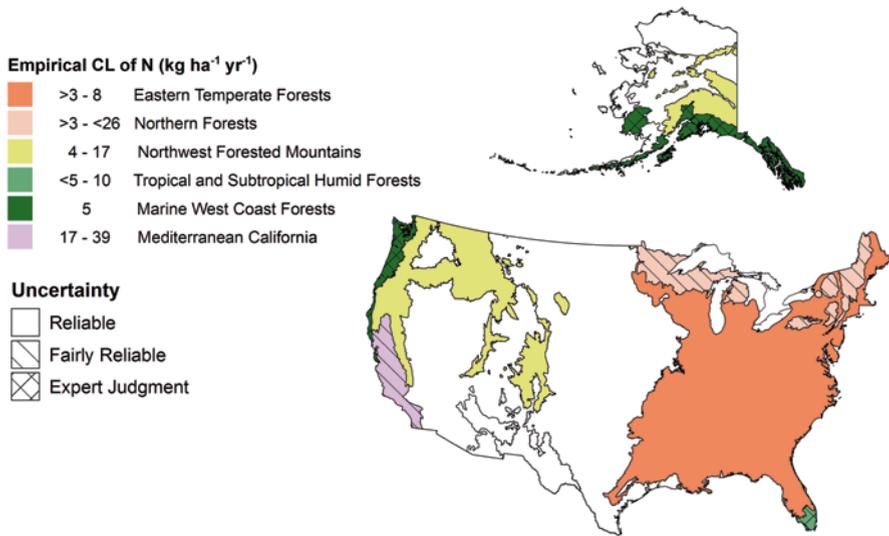


Fig. 5.6 Map of critical loads for forest ecosystems by ecoregion in the United States (This map does not include the responses of mycorrhizal fungi, lichens, or understory herbaceous plants already represented; see Fig. 5.3 for legend explanations)

the lower end of the range representing Northern and Eastern Forests, the upper end representing Mediterranean California mixed conifers (Fig. 5.6). At $4 \text{ kg N ha}^{-1} \text{yr}^{-1}$ in the Colorado Rockies, increasing NO_3^- concentration was reported in the organic horizon, which suggests incipient N saturation (Rueth and Baron 2002). The highest critical loads were reported for Mediterranean California mixed conifer forests for forest sustainability and for soil acidification caused by increased N deposition. These sites experience some of the highest N deposition reported in the United States, up to approximately $70 \text{ kg N ha}^{-1} \text{yr}^{-1}$ (Fenn et al. 2008).

Critical loads for forests vary across ecoregions due in part to reported receptors, site and soil characteristics, and background N deposition status. Critical loads values were lower for ecoregions where sensitive forest receptors, such as mycorrhizal fungi (Marine West Coast Forests) were used to set critical loads. Use of forest health and species composition resulted in a large range in critical loads in Northern Forests and Mediterranean California. In the Northwestern Forested Mountains, the critical load based on NO_3^- leaching ranged from a low value of $4 \text{ kg ha}^{-1} \text{yr}^{-1}$ in subalpine forests to $17 \text{ kg ha}^{-1} \text{yr}^{-1}$ in mixed conifer forests.

5.6 Freshwater and Wetland Ecosystems

Freshwater lakes and streams, and wetlands (freshwater and estuarine intertidal) are ecosystem types that occur in most ecoregions in North America. In freshwater lakes and streams, phytoplankton, algae that live in the water column, are sensitive

to the chemical environment in which they reside, and many species can be used as indicators of the levels of nutrients or acidity because of individual species' preference for specific chemical conditions. Diatoms are used in this discussion because there has been more work published on these algae than others, but other types of algae also respond to N deposition (Lafrancois et al. 2004; Michel et al. 2006). Of the wetlands which occur in the conterminous United States, 95% are freshwater and 5% are estuarine or marine (USDI FWS 2005). The species composition differs between freshwater and intertidal wetlands, although together they support more than 4200 native plant species. Despite the high biodiversity, the effects of N loading are studied in just a few plant species.

5.6.1 *Effects of Nitrogen Deposition*

For the analysis of nutrient N effects to freshwater lakes and streams, we relied on papers and studies that linked aquatic biological and ecological response to atmospheric deposition, but the results are consistent with laboratory or *in situ* dose-response studies and even land use change studies. The productivity of minimally disturbed aquatic ecosystems is often limited by the availability of N, and slight increases in available N trigger a rapid biological response that increases productivity and rearranges algal species assemblages (Nydick et al. 2004; Saros et al. 2005). The mechanism for change is alteration of N:P ratios, which can increase productivity of some species at the expense of others (Elser et al. 2009). As with the terrestrial systems described above, the nutrient responses of lakes and streams are most evident where land use change and acidic deposition have been limited, thus most evidence of exceedance of critical loads comes from high elevations of the western United States (Baron et al. 2011). As with terrestrial plants, some diatoms respond rapidly to an increase in available N. An example that has been observed from a number of different lakes of the Rocky Mountains is dominance of two diatoms (*Asterionella formosa* and *Fragilaria crotonensis*) in lakes with higher N, in contrast to the flora of lakes with lower N deposition where there is a more even distribution, thus high biodiversity, of diatoms. Higher trophic levels (zooplankton, macroinvertebrates) may be secondarily affected by N, but further increases in primary, or autotrophic, production will be limited by other nutrients such as P or silica (Si).

Both freshwater and estuarine intertidal wetlands tend to be N-limited ecosystems (LeBauer and Treseder 2008; U.S. EPA 1993). Known responses to N enrichment are generally derived from nutrient-addition studies in the field and observations along gradients of N deposition. A variety of ecological endpoints are evaluated, such as altered soil biogeochemistry, increased peat accumulation, elevated primary production, changes in plant morphology, changes in plant population dynamics, and altered plant species composition (U.S. EPA 2008). In general, the sensitivity of wetland ecosystems to N is related to the fraction of rainfall (a proxy for atmospheric N deposition) in the total water budget. Most freshwater wetlands, such as bogs, fens, marshes and swamps, have relatively closed water and N cycles,

thus are more sensitive to N deposition than estuarine intertidal wetlands, such as salt marshes and eelgrass beds (Greaver et al. 2011).

5.6.2 Critical Loads of Nitrogen

In general, critical loads for freshwater lakes and streams tend to be low, because the target organisms are unicellular algae that respond rapidly to changes in their chemical environment. The range of critical loads for eutrophication and acidity in freshwaters is 2–9 kg N ha⁻¹yr⁻¹ (Baron et al. 2011); the range reported for terrestrial ecosystems is much broader (Table 5.1; Fig. 5.7). Critical loads for NO₃⁻ leaching from terrestrial ecosystems ranged from 4–17 kg N ha⁻¹yr⁻¹, but many sensitive freshwaters at high altitudes are found above the tree-line where few watershed buffering mechanisms exist, due to sparse vegetation, poorly developed soils, short hydraulic residence time, and steep topography. These factors influence how rapidly a system exhibits elevated N leaching in response to increased N deposition, and how this increased N availability subsequently influences biota. In general, lakes have relatively rapid N turnover times compared to soil N pools and are at least seasonally well-mixed. They would thus be expected to have lower critical loads. Thus responses of terrestrial plants would not be expected to be as rapid as those of freshwater organisms.

Generally, freshwater wetlands are more sensitive to N deposition than estuarine intertidal wetlands, with critical loads for freshwater wetlands that range

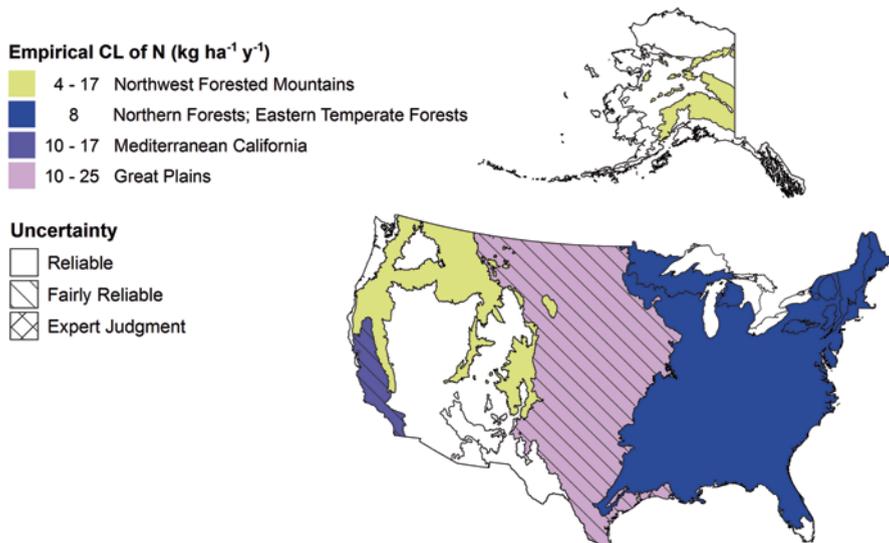


Fig. 5.7 Map of critical loads for freshwater and wetland ecosystems based on increased nitrate leaching by ecoregion in the United States (see Fig. 5.3 for legend explanations)

from 2.7–14 kg N ha⁻¹yr⁻¹ (Table 5.1; Greaver et al. 2011). The bryophyte genus *Sphagnum* and the carnivorous pitcher plant are the two taxa most commonly studied. The critical loads reported for freshwater wetlands (Greaver et al. 2011) fall between those reported for inland surface waters (Baron et al. 2011) and those reported for terrestrial ecosystems (Pardo et al. 2011c). This pattern may be related to the rate of N released by soils/sediment to the ecosystem. The critical load tends to be higher for estuarine intertidal wetlands than other types of ecosystems because they have open nutrient cycles which are often strongly affected by N loading sources other than atmospheric deposition. Based on field observations of N loading effects on plant growth and species composition on salt marsh and eel grass habitat, the critical load for estuarine intertidal wetlands ranges between 50–400 kg N ha⁻¹yr⁻¹ (Table 5.1).

5.7 Discussion and Conclusions

5.7.1 *Effects of Nitrogen Deposition*

The most significant changes that we are currently observing in the United States in response to elevated N deposition are changes in species composition: losses of N-sensitive species, shifts in dominance, and losses of native species in favour of exotic, invasive species. Shifts in diatom and lichen community composition away from N-intolerant (oligotrophic) species are observed across the country. Alterations in herbaceous species are broadly observed, but are not always clearly documentable because of the long-term pollution inputs and other disturbances (including land-use change) that caused changes prior to the initiation of careful observations.

Numerous examples illustrate the significance of these species- and community-level effects. In serpentine grasslands in California, it was clearly demonstrated that unless N inputs are decreased or N is removed in biomass, a larval host plant and numerous nectar source plants utilized by a threatened and endangered butterfly will decrease to levels unable to sustain the checkerspot butterfly population (Fenn et al. 2010; Weiss 1999). In Joshua Tree National Park in southern California, N deposition favours the production of sufficient invasive grass biomass to sustain fires that threaten the survival of the namesake species (Fenn et al. 2010; Rao et al. 2010). Other sensitive ecosystems include alpine meadows, where relatively low levels of N deposition have already changed species composition (Bowman et al. 2006). Changes in historical diatom community composition from N-limited to N-tolerant species have been observed in lake sediment cores at many locations in the western United States, providing early evidence of freshwater ecosystem eutrophication (Wolfe et al. 2001; 2003).

Changes in ecosystem structure are linked to changes in ecosystem function. For example, extirpation of lichens can alter food webs by reducing the availability of nesting material for birds, invertebrate habitat, and critical winter forage for

mammals, and can also affect nutrient cycling (Cornelissen et al. 2007). In some arid low-biomass California ecosystems, N-enhanced growth of invasive species results in increased fire risk, even in areas where fire is normally infrequent (Allen et al. 2009; Fenn et al. 2010; Rao et al. 2010).

There is also evidence of N deposition contributing to multiple stress complexes, resulting in reduced forest sustainability (Grulke et al. 2009; McNulty and Boggs 2010). In North Carolina, elevated N deposition predisposed a pine ecosystem to a pest outbreak following a drought (McNulty and Boggs 2010). These types of complex interactions may be difficult to predict, but may intensify the impact of elevated N deposition in concert with other stressors, including climate change (Wu and Driscoll 2010). Further examples of changes in ecosystem structure and function are observed in coastal areas, where increased N export has led to toxic algal blooms (Rabalais 2002). As an example of N deposition effects on trace gas chemistry and climate change, N loading to ecosystems results in increased emissions of N trace gases, such as NO (nitric oxide, an ozone precursor), N₂O (nitrous oxide, a long-lived and powerful greenhouse gas); as well as declines in soil uptake of CH₄ (methane, another long lived and powerful greenhouse gas) (e.g. Liu and Greaver 2009).

5.7.2 Relative Sensitivities of Different Receptors, Ecosystem Types, and Regions

This synthesis demonstrates that empirical critical loads of N differ among life forms, tending to increase in the following sequence: diatoms < lichens and bryophytes < mycorrhizal fungi < herbaceous plants and shrubs < trees. Nitrogen deposition more rapidly affects those species that experience the most direct exposure to elevated N levels in the atmosphere (lichens and bryophytes) or receiving waters (diatoms), especially for those organisms that lack protective structures. By contrast, the capacity of soil organic matter to accumulate large quantities of N may delay adverse impacts on many herbs, shrubs, and trees. Altered N availability often appears to shift species composition most rapidly within those communities dominated by species with short lifespans (diatoms) compared to those with long lifespans (trees).

Critical loads vary more by receptor and response type than by region. For the same response of a given receptor, the western U.S. has generally similar critical load values to the eastern U.S., with the apparent exception that the critical load for NO₃⁻ leaching is approximately twice as high in Mediterranean California mixed conifers compared to northeastern forests (Fig. 5.7). In contrast, the critical load for NO₃⁻ leaching in high elevation catchments in the Colorado Front Range are lowest in the U. S., likely attributable to low biological N retention and storage capacity in these steep, rocky catchments (Baron et al. 2000; Fenn et al. 2003a, b; Sickman et al. 2002; Williams and Tonnessen 2000).

5.7.3 *Factors Affecting the Critical Load*

Multiple abiotic and biotic factors affect the critical load (Table 5.2). Abiotic influences include a range of climatic, hydrologic, and soil factors that can affect the timing and magnitude of N delivery to sensitive receptors. Climatic factors include temperature, precipitation amount and distribution, and the extent and rate of climate change. Hydrologic factors include catchment size, topographic relief, and flow path. Soil factors include soil type, age, depth, coverage, and parent material. Disturbance—forest fires or cutting—and past agricultural use can also affect soil N and thus the critical load.

Biological factors likely to contribute to lower critical loads of N include particularly sensitive species (diatoms, lichens, mycorrhizal fungi, certain plants), single species versus community responses, low biomass and low productivity ecosystems, short lifespan of receptor of concern, presence of invasive species, and presence of ozone-sensitive species (Fenn et al. 2008; Grulke et al. 1998, 2009; Grulke and Balduman 1999). For example, low-biomass ecosystems (e.g., grasslands, coastal sage scrub, desert) are more sensitive to N-enhanced growth of invasive species, if invasive pressure occurs. These low-biomass ecosystem types sometimes occur because of warm and dry climatic conditions. Because warmer temperatures often correspond to greater metabolic rates, longer periods of biological activity, greater biomass, and more rapid N cycling, one might expect that the critical load would increase with increasing temperature as has been suggested in Europe (Bobbink et al. 2003). We do not observe such a pattern across U.S. ecoregions in the critical loads reported in this synthesis, but Europe does not have warm and dry deserts with low critical loads as does the U.S. Note, however, that the uncertainty of the critical load estimates varies and is often fairly high, which may make it difficult to discern patterns in critical load values across regions. Moreover, a temperature pattern may be confounded by gradients in deposition form and quantity, moisture and elevation.

5.7.4 *Comparison to Critical Loads in Europe*

The range of critical loads of N deposition in U.S. ecoregions for terrestrial ecosystems is 1–39 kg N ha⁻¹yr⁻¹, which is close to the range for the most recently reported critical loads values for similar ecosystems in Europe (Bobbink and Hettelingh 2011). However, the low end of the critical loads range is nearly always lower in the U.S. than in Europe (Fig. 5.8; Table 5.3). There are several potential reasons why critical loads for the U.S. remain lower than European critical loads. These includes greater availability of pristine baselines in the U.S., more intensive land use in Europe; greater dominance of N deposition by reduced forms of N in Europe, and different threshold criteria.

Table 5.2 Assessment and interpretation of empirical critical loads of nutrient N for North American ecoregions

Ecoregion	Factors affecting the range of CL ^a	Comparison within ecoregion ^b
Tundra	<ol style="list-style-type: none"> 1) Moisture 2) Competition between vascular plants and cryptogams 3) P-limitation 4) Temperature 5) pH 	<p>Critical loads are higher in wet and P-limited tundra; acidic tundra may be more sensitive to N deposition than non-acidic tundra. Increased N deposition may be more detrimental to lichens in the presence of graminoids and shrubs in the low and mid arctic than to lichens with less competition in the high arctic. Response time increases with latitude due to colder temperatures, less light, and poorer N and P mobilization</p>
Taiga	<ol style="list-style-type: none"> 1) Soil depth 2) Vegetation type and species composition 3) latitude 	<p>Morphological damage to lichens has been observed at a lower deposition in forests and woodlands than in shrub lands, bogs or fens; cryptogam dominated mats on thin soils become N saturated faster than forest islands</p>
Northern Forest	<ol style="list-style-type: none"> 1) Receptor 2) Tree species 3) Stand age 4) Site history 5) Pre-existing N status 	<p>CLs for lichen are generally lowest, followed by CLs for ectomycorrhizal fungi and NO₃⁻ leaching. CLs for herbaceous species and forests are generally higher than for other responses</p>
Northwest Forested Mountains	<ol style="list-style-type: none"> 1) Biotic receptor 2) Accumulated load of N 3) Ecosystem 4) Region 	<p>In alpine regions, diatom changes in lakes are seen at the lowest CL. Changes in individual plants are seen next, followed by vegetation community change, then soil responses. In subalpine forests, the CL of 4 kg N ha⁻¹yr⁻¹ for foliar and soil chemistry changes is similar to the lichen CL of 3.1–5.2 kg N ha⁻¹yr⁻¹ for lichen community change</p>
Marine West Coast Forests	<ol style="list-style-type: none"> 1) Background N status 2) Soil type 3) Species composition 4) Fire history 5) Climate 	<p>The midrange of responses reported for lichens (2.7–9.2 kg N ha⁻¹yr⁻¹) is broadly comparable to that for plant, soil, and mycorrhizal responses (5 kg N ha⁻¹yr⁻¹), despite limited studies for non-lichen responses.</p>
Eastern Forests	<ol style="list-style-type: none"> 1) precipitation 2) soil cation fertility and weathering 3) Biotic receptors 	<p>CLs for NO₃⁻ leaching, lichen community change, and ectomycorrhizal fungal response are within the same range. Arbuscular mycorrhizal fungal and herbaceous CLs are higher</p>

Table 5.2 (continued)

Ecoregion	Factors affecting the range of CL ^a	Comparison within ecoregion ^b
Great Plains	<ol style="list-style-type: none"> 1) N status 2) Receptor 3) Precipitation 	<p>Comparison within ecoregion^b</p> <p>CLs are lower in the tall grass prairie than in the mixed- and short-grass prairies. CLs in tall- and mixed-grass prairie are lower on N poor sites and sites with very N responsive plant species. CL in the short-grass prairie is likely lower in wet years than in dry years</p>
North American Deserts	<ol style="list-style-type: none"> 1) Receptor 2) Interaction of annual grasses with native forb cover 3) Precipitation 	<p>The lichen CL is lowest, at 3 kg N ha⁻¹yr⁻¹; vegetation CL varies from 3–8.4 kg N ha⁻¹yr⁻¹</p>
Mediterranean California	<ol style="list-style-type: none"> 1) Presence of invasive exotic annual grasses interacting with a highly diverse native forb community 2) N-sensitivity of mycorrhizal fungi 3) N-sensitivity of lichens 4) N retention capacity of catchments, catchment size 5) Co-occurrence of ozone and ozone-sensitive tree species 	<p>The lowest CLs in Mediterranean California are for sensitive lichen in chaparral and oak woodlands and mixed conifer forests. The CL for plant and mycorrhizal fungal community change in coastal sage scrub is higher, at 7.8–10 kg ha⁻¹yr⁻¹. CL for NO₃ leaching is lower in chaparral and oak woodlands (10–14 kg ha⁻¹yr⁻¹) than in mixed conifer forests (17 kg ha⁻¹yr⁻¹). CLs are highest for mixed conifer forest plant community change and sustainability. Fine root biomass in ponderosa pine is reduced by both ozone and elevated soil N</p>
Wetlands	<ol style="list-style-type: none"> 1) Vegetation species 2) The fraction of rainfall in the total water budget 3) The degree of openness of N cycling 	<p>CL is much higher for intertidal wetlands (50–400 kg N ha⁻¹yr⁻¹) than for freshwater wetlands (2.7–14 kg N ha⁻¹yr⁻¹), which have relatively closed water and N cycles</p>
Freshwaters	<ol style="list-style-type: none"> 1) Extent of upstream vegetation development 2) Topographic relief 3) Land use/deposition history 	<p>CLs are lower in western mountain lakes/streams with poorly vegetated watersheds and steep catchments. CLs are greater in eastern lakes with prior land use and decades of acidic deposition</p>

^a Factors causing the critical load (CL) to be at the low or high end of the range reported

^b Comparison of values and causes for differences if multiple critical loads are reported for an ecoregion

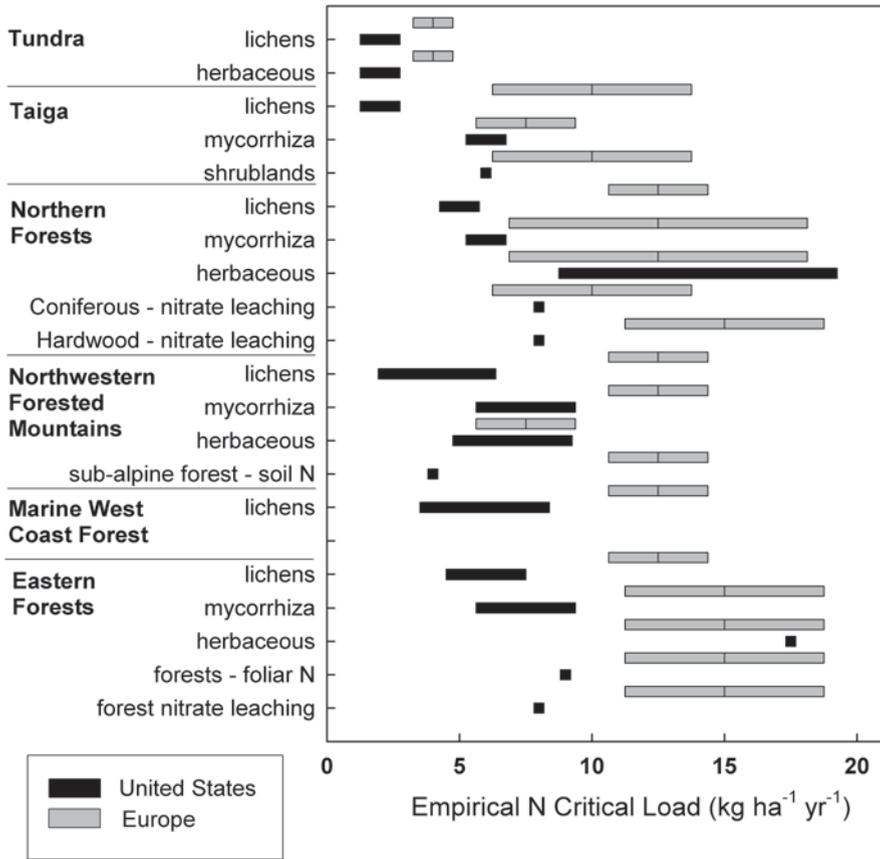


Fig. 5.8 Comparison of empirical critical loads of nutrient nitrogen for Europe. (based on Bobbink and Hettelingh 2011) and the United States

Availability of Pristine Baselines and Studies at Low Deposition: Because of high historic deposition levels, many European systems lack pristine baseline ecosystems as a reference to compare to those experiencing elevated N deposition. For example, past European critical loads for lichens were much higher than those in the U.S. (Bobbink et al. 2003). These loads were influenced by study sites in Scotland experiencing a deposition gradient from 10–22 kg N ha⁻¹yr⁻¹ from which critical loads were set at 11–18 kg N ha⁻¹yr⁻¹ (Mitchell et al. 2005). However, no oligotrophic species were observed, presumably because they were eliminated prior to the initial studies. The more recently reported European critical loads (Bobbink and Hettelingh 2011), used in our comparison, were set at 5–10 kg N ha⁻¹yr⁻¹. In some European ecosystems, such as dry grass lands, there is, however, still a need for more low N addition and deposition experiments (Bobbink and Hettelingh 2011).

Table 5.3 Critical loads for European ecosystems compared to critical loads for U.S. Ecoregions

European Ecosystem type (EUNIS code)	Critical load	Reliability	Indication of exceedance	U.S. Ecoregion; Ecosystem component	Critical load	Reliability	Indication of exceedance
Permanent oligotrophic lakes, ponds, and pools (C1.1)	3–10	##	Change in the species composition of macrophyte communities, increased algal productivity and a shift in nutrient limitation of phytoplankton from N to P	Aquatic; eastern and western high elevation lakes	2–8	#	Increased productivity, eutrophication, altered algal species assemblages
Raised and blanket bogs (D1)	5–10	##	Increase in vascular plants, altered growth and species composition of bryophytes, increased N in peat and peat water	Wetlands; bogs, fens, and swamps	2.7–14	#	Alterations in sphagnum accumulation and net primary productivity; alteration in threatened <i>Sarracenia purpurea</i> community
Sub-Atlantic semidry calcareous grasslands (E1.26)	15–25	##	Increase in tall grasses, decline in diversity, increased mineralization, N leaching; surface acidification	Great Plains; mixed-grass prairie	10–25	#	Change in soil NO ₃ ⁻ pools, increased leaching, plant community shifts
Non-Mediterranean dry acidic and neutral closed grasslands (E1.7)	10–15	##	Increase in graminoids, decline in typical species, decrease in total species richness	Great Plains; tall-grass prairie	5–15	#	Change in biogeochemical N cycling, plant and insect community shifts
Tundra (F1)	3–5	#	Changes in biomass, physiological effects, changes in species composition in bryophyte layer, decrease in lichens	Tundra; prostrate dwarf shrub, lichens	1–3	#	Changes in lichen, bryophyte, and vascular plant cover. Changes in vascular plant CO ₂ exchange, foliar N, and community composition; change in lichen pigment production and ultrastructure
Arctic, alpine, and subalpine scrub habitats (F2)	5–15	#	Decline in lichens, bryophytes and evergreen shrubs	Taiga; shrublands—lichen, moss, and algae	1–6	#	Change in shrub and grass cover, increased parasitism of shrubs; changes in alga, bryophyte, and lichen community composition, cover, tissue N, or growth rates

Table 5.3 (continued)

European Ecosystem type (EUNIS code)	Critical load	Reliability	Indication of exceedance	U.S. Ecoregion, Ecosystem component	Critical load	Reliability	Indication of exceedance
Broadleaved deciduous woodland (G1)	10–20	##	Changes in soil processes, nutrient imbalance, altered composition mycorrhiza and ground vegetation	Eastern and Northern Forests; hardwood forest, southeast coastal plain	3–21	#	Change in mycorrhizal fungal community structure and biomass, change in herb layer and loss of prominent species, increased surface water NO_3^- leaching, increased foliar N, change in tree growth and mortality
Coniferous woodland (G3)	5–15	##	Changes in soil processes, nutrient imbalance, altered composition mycorrhiza and ground vegetation	Northern Forests; coniferous forest	3–26	#	Change in mycorrhizal fungal community structure, biomass decline in arbuscular mycorrhizal fungi, loss of prominent herbaceous species, increased surface water NO_3^- leaching, change in tree growth and mortality
Abies and Picea woodland (G3.1)	10–15	(#)	Decreased biomass of fine roots, nutrient imbalance, decrease in mycorrhiza, changed soil fauna	Northwestern Forested Mountains; subalpine forest	4	##	Increase in organic horizon N; higher net N mineralization rates
Spruce taiga woodland (G3.A)	5–10	##	Changes in ground vegetation, decrease in mycorrhiza, increase in free living algae	Taiga; spruce-fir forests	5–7	(#)	Change in ectomycorrhizal fungal community structure
Temperate and boreal forest; lichen and algae (G)	5–10	#	Decline in lichens, increase in free-living algae	Eastern and Northern Forests, Northwestern Forested Mountains, Marine West Coast Forest; lichens	1–9	#	Lichen community change

reliable, # fairly reliable, (#) expert judgment

Land Use: A larger fraction of the forested landscape in Europe is heavily managed (harvested and planted) relative to the U.S. High rates of harvest removals of N in biomass, creating greater N demand and storage during re-establishment of the forest stand could contribute to higher critical loads in Europe than the U.S.

Forms and Mode of Measurement of N inputs: NH_4^+ inputs tend to be higher and represent a greater proportion of total N inputs in Europe, particularly in past decades; this is changing in the U.S. Some receptor species can be more sensitive to reduced than to oxidized forms of N inputs, and nitrification of NH_4^+ inputs can accelerate ecosystem acidification relative to inputs of NO_3^- .

Threshold Criteria: Another possible explanation for the higher critical loads is that the response thresholds utilized in Europe are sometimes higher. For example, choosing a threshold of a shift in lichen community composition will produce a much lower critical load than a threshold of near extirpation of lichen species as used in earlier European work (Bobbink et al. 2003). As a second example, choosing a threshold of initial changes in N biogeochemistry in the Colorado Front Range, interpreted as incipient responses of N saturation, led to a critical load $<4 \text{ kg N ha}^{-1}\text{yr}^{-1}$ (Rueth et al. 2003). This is a subtle initial N enrichment response when compared to the magnitude of change (a later stage of N saturation) for the critical loads thresholds in Europe ($10\text{--}15 \text{ kg ha}^{-1}\text{yr}^{-1}$). Finally, much of the same research was used to set critical loads for both European and U.S. tundra and taiga ecosystems (Bobbink and Hettelingh 2011; Pardo et al. 2011c). The difference in the critical loads for these ecosystems is primarily due to different threshold criteria.

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