

19 SYNTHESIS

L.H. Pardo, L.H. Geiser, M.E. Fenn, C.T. Driscoll, C.L. Goodale, E.B. Allen, J.S. Baron, R. Bobbink, W.D. Bowman, C.M. Clark, B. Emmett, F.S. Gilliam, T. Greaver, S.J. Hall, E.A. Lilleskov, L. Liu, J.A. Lynch, K. Nadelhoffer, S.S. Perakis, M.J. Robin-Abbott, J.L. Stoddard, K.C. Weathers

19.1 Background

19.1.1 Effects of Nitrogen Deposition on Ecosystems

Human activity in the last century has led to a substantial increase in nitrogen (N) emissions and deposition (Galloway et al. 2003). Because of past, and, in some regions, continuing increases in emissions (Lehmann et al. 2005, Nilles and Conley 2001), this N deposition has reached a level that has caused or is likely to cause alterations and damage in many ecosystems across the United States. In some ecoregions, the impact of N deposition has been severe and has changed the biotic community structure and composition of ecosystems. In the Mediterranean California ecoregion, for example (see Chapter 13), replacement of native by exotic invasive vegetation is accelerated because exotic species are often more productive under elevated N deposition than native species in some California grasslands, coastal sage scrub, and desert scrub (Fenn et al. 2010, Rao and Allen 2010, Rao et al. 2010, Weiss 1999, Yoshida and Allen 2004). Such shifts in plant community composition and species richness can have consequences beyond changes in ecosystem structure: shifts may lead to overall losses in biodiversity and further impair particular threatened or endangered species (Stevens et al. 2004). The extirpation of the endangered checkerspot butterfly (*Euphydryas editha bayensis*), because the host plant for the larval stage disappears in N-enriched ecosystems (Fenn et al. 2010, Weiss 1999), is just one example of the detrimental impacts of elevated N deposition.

In addition to altering ecosystem structure, N deposition can also affect ecosystem function, affecting N-cycle processes such as N mineralization, nitrification rates, and nitrate (NO₃⁻) leaching rates, as well as plant tissue N concentration. These changes indicate early stages of N saturation. Nitrogen saturation is the series of ecosystem changes that occur as available N exceeds plant and microbial demand (Aber et al. 1989, 1998). In

some cases, these early responses may lead to a cascade of alterations in the N cycle that ultimately affect the function or structure of the ecosystem (Galloway et al. 2003). For example, elevated N inputs may lead to plant nutrient imbalances, which then increase plant susceptibility to inciting stressors such as cold, drought, or pests (Bobbink et al. 1998, Schaberg et al. 2002). This series of responses was observed in a southern Vermont montane red spruce (*Picea rubens*) stand, where increased foliar N concentration was associated with reductions in foliar membrane-associated calcium (Ca) and decreased cold tolerance, which resulted in increased winter injury (Schaberg et al. 2002). Another example of the N cascade (Galloway et al. 2003) is increased soil NO₃⁻ leaching, which can result in episodic acidification of surface waters, harming fish species (Baker et al. 1996). Other responses to low levels of elevated N deposition, such as increased plant growth and increased carbon (C) sequestration by trees (Thomas et al. 2010), may be perceived as beneficial where forests are managed for tree growth. In other instances, it is not known whether the early indicators of N saturation will be followed by other effects. In these cases, the perceived extent of harm caused by N deposition depends, in part, on which ecosystem service is of particular value for different stakeholders. For example, the level or type of change or harm that is unacceptable may vary according to resource management goals. In a conservation area, for example, any alteration in N cycling may be considered unacceptable, whereas for other land areas, changes of a certain magnitude or scope may be acceptable or even desirable based on resource use (such as timber harvesting) or other factors. Land and resources may be valued for a wide range of purposes, including biodiversity, food and wood production, clean water, and recreation. Quantification and then valuation of these ecosystem services for each land area of interest is required to fully account for impacts of N deposition.

19.1.2 Critical Loads Definition and Previous Uses

One method for evaluating the potential impacts of air pollution on ecosystems is the critical loads approach. The critical load is defined as *the level of a pollutant below which no detrimental ecological effect occurs over the long term according to present knowledge* (UBA 2004). Critical loads have been used most broadly in Europe (Posch et al. 1995, 2001) as a tool in the process of negotiating decreases in air pollution. Critical loads have been more widely applied in Canada than in the United States; critical loads have been published for upland forests (Ouimet et al. 2006) and lakes (Dupont et al. 2005) in eastern Canada and included in European assessments (Hetteling et al. 2008). In the United States, critical loads have been calculated for specific regions such as the northeastern United States (Dupont et al. 2005, NEG/ECP 2003), California (Fenn et al. 2008, 2010), and Colorado (Baron 2006, Bowman et al. 2006, Williams and Tonnessen 2000), and, at a coarse scale, the conterminous United States (McNulty et al. 2007). Critical loads are of interest to policy makers for assessing emission control programs and to natural resource managers as a tool to evaluate the potential impact of new pollution sources (Burns et al. 2008, Environment Canada 2008, Lovett and Tear 2008, Lovett et al. 2009, Porter et al. 2005, US EPA 2007, US EPA 2008). Critical loads are also used by policy makers and resource managers to establish benchmarks for resource protection and to communicate the impacts of deposition on natural resource conditions. The development and use of critical loads provides a framework in which the research community collaborates with natural resource managers to quantify the effects of air pollution on ecosystems and help guide emission control programs. As a result, scientific progress, international collaboration, and interactions between researchers and policy makers are enhanced. Likewise, as a result of this focus on developing critical loads, the results of scientific studies are more broadly applied toward ecosystem protection by land managers, policy makers, and regulators.

Critical loads have been determined most frequently in the United States for effects of acidity (NEG/ECP 2003, Sullivan et al. 2005), but are also being increasingly

used in evaluating impacts of excess N deposition on ecosystems (Fenn et al. 2008, 2010). Empirical critical loads are determined from observations of detrimental responses of an ecosystem or ecosystem component to a given, observed N deposition input (Pardo 2010). This level of N deposition is set as the critical load and extrapolated to similar ecosystems. Empirical critical loads for N, which are set based on field evidence, have been used in Europe since the 1990s (Bobbink et al. 1992, 2003, 2010). Empirical critical loads are particularly valuable because they are based on actual observations of detrimental effects to ecosystems by N deposition. Other approaches include the steady-state mass balance method (UBA 2004) and dynamic modeling (de Vries et al. 2010, Slootweg et al. 2007), both of which have been used broadly in Europe. Steady-state mass balance modeling is based on estimating the net loss or accumulation of N inputs and outputs over the long term under the assumption that the ecosystem is at steady-state with respect to N inputs. Dynamic models also use a mass balance approach, but consider time-dependent processes and require detailed data sets for parameterization and testing (Belyazid et al. 2006, de Vries et al. 2007).

Exceedance of the critical load is defined as the current deposition minus critical load; when exceedance is greater than zero, the ecosystem is susceptible to harmful ecological effects. The exceedance is useful in communicating the extent of risk to ecosystems under current and future deposition scenarios. The target load is a level of deposition set by policy makers to protect sensitive ecosystem components. The target load can be set below the critical load in order to eliminate exceedance within a given time period.

19.1.3 Objectives

The objective of this project is to synthesize current research relating atmospheric N deposition to effects on terrestrial and aquatic ecosystems in the United States and to identify empirical critical loads for atmospheric N deposition where possible. In this final chapter, we summarize the critical loads reported for all the ecoregions of the United States, discuss the abiotic and biotic factors that affect the critical load for N within

each ecoregion, compare critical loads by life form or ecosystem compartment (mycorrhizal fungi, lichens, herbaceous species, and trees/forest ecosystems) across all ecoregions, and compare critical loads in the United States to those for similar ecoregions or ecosystems in Europe. Finally, we discuss the significance of these findings and the highest priorities for future research.

19.2 Approach

For this assessment, we report responses to N inputs for ecoregions that occur in the United States based on the Commission for Environmental Cooperation (CEC) for North America Level I map of ecoregions for North America (CEC 1997; Figures 2.1 and 2.2; see Chapter 2). The approach we used was to identify the receptor of concern (organism or ecosystem compartment), the response of concern, the critical threshold value for that response, which studies could be utilized, and the criteria for setting the critical load and extrapolating it to other sites or regions. These methods are described in detail in Chapter 4.

The receptors that we evaluated included freshwater diatoms, mycorrhizal fungi and other soil microbes, lichens, bryophytes, herbaceous plants, shrubs, and trees. We also considered biogeochemical processes within the ecosystem. The main responses reported fell into two categories: (1) biogeochemical; and (2) individual species, population, and community responses. Biogeochemical responses included increased N mineralization and nitrification (and N availability for plant and microbial uptake), increased gaseous N losses (ammonia (NH₃) volatilization, nitric oxide (NO) and nitrous oxide (N₂O) from nitrification and denitrification), and increased N leaching. Individual species, population, and community responses included increased tissue N concentration, physiological and nutrient imbalances, altered growth, altered root:shoot ratios, increased susceptibility to secondary stresses, altered fire regimes, changes in species abundance, shifts in competitive interactions and community composition, and changes in species richness and other measures of biodiversity, and increases in invasive species.

We considered experimental N-addition studies, N-deposition gradient studies, and long-term monitoring studies in order to evaluate ecosystem response to N-deposition inputs. Most of these studies were not designed to quantify critical loads, which presented some challenges. We afforded greater weight to long-term fertilization studies (5 to 10 years) than to short-term studies, although short-term studies were also considered when other observations were scarce. Single-dose forest fertilization studies exceeding 50 kg N ha⁻¹ were generally not considered. When studies were designed to determine critical loads, the addition levels generally depicted modest increases above ambient deposition, and were more likely to have smaller increments between the treatment levels, multiple (three or more) treatment levels, and, ideally, treatments spanning the critical load. In such cases, our estimates of the critical load are made with greater certainty than with other approaches. Nitrogen gradient studies implicitly include long-term exposure to pollutants and therefore are more likely than N manipulation studies to depict conditions that are near steady-state with respect to ambient N inputs. Long-term monitoring studies sometimes offer the opportunity to observe changes over time in response to increasing or elevated N-deposition inputs. We estimated critical loads based on data from >3200 sites (Figure 3.1).

The critical threshold of the response parameter is the threshold value at which an acceptable response is still observed. For example, when lichens are the receptors of concern and the response variable is thallus N concentration, the critical threshold is the highest value of thallus N concentration that represents a desirable condition: the critical threshold is reported as 1 percent for a recent study (Fenn et al. in 2008). The critical threshold is also referred to as the critical limit (UBA 2004). The critical threshold is different from the critical load; in this case, the critical load is the deposition at which the lichen thallus N concentration has reached or exceeded the critical threshold of 1 percent.

In general, we determined the critical load based on the observed response pattern. 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 and the deposition level that corresponded to a departure from that state. The criteria for setting critical loads are discussed in detail in Chapter 4.

19.3 Deposition

Total N emissions have increased substantially since the 1950s (Galloway 1998, Galloway et al. 2003). As S deposition has declined in response to U.S. Federal emission control programs, the magnitude of N relative to S deposition has increased since the 1980s (Driscoll et al. 2003). More recently, the relative proportion of NH_x (ammonium (NH_4^+) and ammonia (NH_3)) to NO_x (nitric oxide (NO) and nitrogen dioxide (NO_2)) emissions has also increased for many areas of the United States (Kelly et al. 2005, Lehmann et al. 2005).

In order to quantify the critical load, we generally used the deposition reported in the publication or, when that was not available, we used modeled deposition (e.g., Community Multiscale Air Quality [CMAQ] model, ClimCalc [Ollinger et al. 1993], National Atmospheric Deposition Program [NADP; NADP 2009] maps). The different forms of N deposition included in this assessment for estimating critical loads are: wet, bulk, wet plus dry, throughfall, and total (wet plus dry plus cloud/fog) inorganic N deposition. Total N deposition is considered the most appropriate value to use in evaluating ecosystem responses, however, in many studies this information is not available. Throughfall N is generally considered a good surrogate for total N deposition, because it typically does not underestimate total N inputs as much as wet or bulk deposition and it is a good estimate of N delivered to the forest floor (Weathers et al. 2006). However, because of the potential for canopy uptake and transformation of N, throughfall is usually considered as a lower-bound estimate of total N deposition. None of the studies include reported inputs of organic N, so this report focuses on responses to inputs of inorganic N. Deposition used to calculate exceedance at sites included in this analysis (Chapter 3) was quantified by the CMAQ model v.4.3 (hereafter CMAQ 2001 model,

which uses 2001 reported data) (Byun and Ching 1999, Byun and Schere 2006) simulations of wet plus dry deposition of N species (Figure 3.1).

We rarely had sufficient data to distinguish plant or ecosystem response to reduced forms (NH_x) versus oxidized forms (NO_y : NO, NO_2 , nitric acid (HNO_3), organic and inorganic nitrates) of N. There is some evidence that for some species, reduced forms of N may have more substantial impacts than oxidized N (Bobbink et al. 2003, Kleijn et al. 2008). This differential response may be due to direct toxicity of gaseous NH_3 (Krupa 2003) or the toxicity to some plant species (or their mycorrhizal fungi) of high levels of NH_4^+ in soil, but can also be a result of soil acidification (van den Berg et al. 2005). Lichens in California’s Central Valley (Jovan and McCune 2005) have been shown to be particularly sensitive to total reduced N (i.e. NH_4^+ plus NH_3). Across Europe, lichen responded to NH_3 and to a lesser extent NH_4^+ (Cape et al. 2009, Sutton et al. 2009). Much of the research on NH_3 effects evaluates the response to concentration of NH_3 , which would be used for determining the critical level of NH_3 rather than the critical load. This is an important distinction: the critical level is the atmospheric concentration above which adverse effects to sensitive vegetation may occur (UBA 2004). 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 . Importantly, not all species are more sensitive to NH_x than NO_y ; these responses vary by species and functional type. Some species are more sensitive to increases in NO_y , as was demonstrated for boreal forests by Nordin et al. (2006).

The accuracy of the atmospheric N-deposition values used directly influences the accuracy of critical load and exceedance estimates. Several factors contribute to uncertainty in N-deposition estimates, including sparse data for many ecosystem types, including arid, high elevation sites, and for sites with high inputs from snow or cloudwater/fog deposition, where N deposition tends to be underestimated. In addition, models of deposition

often assume homogenous canopies or terrain, or the output (e.g., CMAQ) is at a spatial scale (grid size) too coarse to capture complex topography and other local influences on deposition (Weathers et al. 2006). These issues are discussed in detail in Chapter 3. When more accurate and precise N-deposition estimates become available, the data presented in this study may be re-evaluated to refine the critical loads estimates.

Note that CMAQ deposition data at a 36 km x 36 km grid were used to calculate exceedances (current deposition—critical load) for this analysis. CMAQ deposition includes dry deposition of NH₃ and trace NO_y species which are not included in many estimates of deposition (including those used to estimate many of the N critical loads in this assessment). Although these N constituents generally make up a small fraction of total estimated N deposition, the use of CMAQ data has the potential to overestimate the area of exceedance. However, some studies suggest CMAQ actually underestimates N deposition (Fenn et al. 2010). The discrepancy between CMAQ estimates and actual deposition would be of greatest concern at sites where NH₃, NO, and NO₂ dry deposition or fog represent a high fraction of inputs. Their inclusion would be most significant where the critical load is lowest. Fortunately, most of the lichen critical loads, which are typically the lowest reported within a given ecoregions (i.e., the most likely to be affected by the slightly higher CMAQ deposition), were determined based on CMAQ inputs. In other instances, for example in the arid West when emissions are high, CMAQ may underestimate total deposition (Fenn et al. 2010).

19.4 Sources of Uncertainty in Empirical Critical Loads Estimates

There are several other sources of uncertainty in our assessment of empirical critical loads, beyond those associated with the measurement of atmospheric deposition. In general, there is a dearth of observations on ecosystem response to inputs near the critical load. To address these data gaps, we suggest priorities for future research below. In some ecoregions, a single study or very few studies are available. If the variability of ecosystem response to N deposition across an

ecoregion is not depicted by the studies available, the estimated critical load for N may be relevant for only a single ecosystem type or a single sub-region within the ecoregion. Without extensive data, it is not possible to know whether a study site is more or less sensitive than other sites in the ecoregion. It is most effective to have a large number of studies which demonstrate the range of responses observed to better define the threshold value (or constrain the deposition range over which the response occurs).

Other sources of uncertainty include time lags in the response to N deposition and the effects of multiple stressors, both of which are artifacts of the empirical approach, and, as such, are difficult to address. However, with more long-term studies and more response data, confidence in these empirical critical load estimates will improve, as has been demonstrated in Europe (Bobbink et al. 1992, 2010). Because ecosystems do not respond instantaneously to changes in N inputs, there are inherent time lags associated especially with N addition studies. These time lags become more important with increasing lifespan or size of organism; a tree will respond more slowly than an herbaceous annual, for example. Time lags also depend on the rate of N input, with lower rates of input typically leading to longer time lags before an initial response (Clark and Tilman 2008). Some species adapted to low nutrient supply also tend to respond slowly to N additions (Theodose and Bowman 1997). (Note that, although the time lag may be longer for these low-N-adapted species, they may still be amongst the most sensitive to small N additions). There may be large differences in responses among species within the same ecosystem, with many species being relatively nonresponsive and a few opportunistic species transforming community structure and function. Ecosystems with inherently large N pools or capacity to absorb N will exhibit longer time lags with respect to changes in N inputs than ecosystems with smaller N storage pools. Thus, it can be difficult to extrapolate the response at a higher dose over a short study to a lower input over the long term (Clark and Tilman 2008). The absence of low N addition studies further complicates interpolation because often N additions are far greater

than the critical load. For both N addition and gradient studies, the reference plot or low end of the deposition gradient may already have been altered from a “pristine” condition. Even for gradient studies, the time lag in response to N deposition must be considered. As the ecosystems in gradient studies are typically still being exposed to elevated N inputs, they are continuously responding to those N inputs, although they have had more time to approach steady-state with the N inputs compared with N addition studies. For N gradient studies, it can also be difficult to sort out the effects of other factors that may also vary along the deposition gradient, such as climate, interannual variation in weather, soils, vegetation, disturbances, and other pollutants. On the other hand, because these variations represent “real-world” conditions—in most locations, multiple stressors co-occur—the critical loads estimated in the presence of these stressors may better protect the ecosystems under the current conditions (Fenn et al. 2008).

Another source of uncertainty in empirical relationships is that they are simply field observations of responses to N inputs, and are often lacking mechanistic explanations. They also can only reflect research done to date, and with the exception of N addition studies, only conditions (N deposition rates) observed to date. Because these factors affect the accuracy of the critical load, we indicate the level of uncertainty in our critical loads tables.

19.5 Advantages of the Empirical Critical Loads Approach

In spite of some of the challenges discussed above, an important advantage of empirical critical loads is that they are based on measurable, physical evidence of ecosystem responses to N inputs. Conceptually, steady-state mass balance models have an advantage over empirical critical loads in terms of estimating long-term sustainability, because they are calculated over the long term. This means that steady-state models are less likely to overestimate the critical load, which can happen with empirical critical loads determined based on a rapidly occurring ecosystem response at a given deposition, although lower levels of atmospheric deposition over

a longer time period will actually generate the same response. Currently in the United States, the uncertainty associated with the steady-state mass balance method is high because data are not available to refine the terms in the equations. In fact, the data assembled for empirical critical loads may be useful in defining the acceptable critical thresholds used in steady-state mass balance critical loads calculations. For example, provisional descriptions of the relationships between soil solution NO_3^- concentration and changes in species composition in The Netherlands (Posch et al. 1993, de Vries et al. 2007), have allowed determination of the critical NO_3^- concentration term used in steady-state calculations of critical loads. Dynamic models for critical loads of N in the United States have been applied on a limited basis (Fenn et al. 2008, Wu and Driscoll 2010). For dynamic modeling of nutrient N critical loads, empirical critical loads and other response data are essential: the current understanding of ecosystem response to N deposition in the United States has not been sufficient to develop dynamic models that characterize the range of effects (for example, changes in biodiversity) such as those utilized in Europe (de Vries et al. 2010, Emmett and Reynolds 2003). Dynamic models must be based on a systematic understanding of the responses and mechanisms for those responses. Dynamic models are necessary to adequately characterize the complexity of N cycling at the ecosystem scale, but the models can only be as good as the data upon which they are based. Thus, empirical critical loads currently provide a uniquely valuable approach for assessing the risk of harm to ecosystems in the United States. This report represents a first step toward that understanding by indicating which data are available for key ecosystems and where dynamic modeling could most profitably be applied in the United States after further data collection.

19.6 Overview of Critical Loads across U.S. Ecoregions

The range of critical loads for nutrient N reported for the U.S. ecoregions, inland surface waters, and freshwater wetlands is 1 to 39 $\text{kg N ha}^{-1} \text{ yr}^{-1}$, while coastal wetlands are between 50 to 400 $\text{kg N ha}^{-1} \text{ yr}^{-1}$ (Table 19.1). This range, excluding coastal wetlands, spans N deposition observed over most of the

country (see Chapter 3). Because N deposition varies considerably by region and the critical load varies both by region and receptor, we present the critical loads and likely risk of exceedance by receptor in section 19.8. The locations for which ecosystem response data were available (Figure 3.1) also vary in density of spatial distribution, which impacts the level of certainty of the empirical critical loads estimates. The basis for the critical loads values (Table 19.1) is discussed in detail in the preceding chapters.

The empirical critical loads for N tend to increase in the following sequence for different life forms: freshwater diatoms, lichens and bryophytes, mycorrhizal fungi, herbaceous plants and shrubs, and trees (see section 19.8). Low biomass ecosystem types (e.g., grasslands, coastal sage scrub, desert) are more sensitive to N-enhanced growth of invasive species (if invasive pressure occurs), leading to vegetation-type change. These vegetation types sometimes occur because of warm and dry climatic conditions. As 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 study, but Europe does not have warm and dry deserts with low critical loads as in the United States. Note, however, that the reliability of the critical load estimates varies and is often fairly low, 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. Critical loads seem to vary more by receptor and response type than by region. The western portion of the United States has generally similar critical loads values to the eastern United States for the same response for a given receptor. The apparent exception is that in forests the critical load for NO_3^- leaching is approximately twice as high in Mediterranean California mixed conifers compared to northeastern forests (see section 19.8 and Figure 19.7). In contrast, the critical load for NO_3^- leaching in high

elevation catchments in the Colorado Front Range is lower than anywhere else in the United States, likely attributable to low biological N retention and storage capacity in these steep, rocky catchments (Baron et al. 2000, Fenn et al. 2003a, Sickman et al. 2002, Williams and Tonnessen 2000).

In this synthesis, we found that higher N critical loads were often reported for regions with higher ambient N deposition, as has been observed outside the United States. One explanation for this pattern is that for ecosystems experiencing elevated N deposition, the current condition already represents a change from the condition prior to elevated N deposition (i.e., a pristine or near-pristine state). This pattern would explain why the empirical critical load is often above the ambient deposition even as that deposition increases in the same ecosystem type across a region. Empirical critical loads for N in Europe (see section 19.9) tend to be higher than those for the United States; in China, they are higher still (Duan 2009). This pattern suggests that sometimes the initial change in the ecosystem was not captured in ecosystem measurements, thus the critical load only prevents further change from the current state. This is even more likely to have occurred at sites in Europe where deposition has been very high. For example, European critical loads for lichens were influenced by a study in Scotland based on a deposition gradient from 10 to 22 kg N ha⁻¹ yr⁻¹ which set critical loads at 11 to 18 kg N ha⁻¹ yr⁻¹ (Mitchell et al. 2005). However, the species composition at all sites across the deposition gradient did not include any oligotrophic species, which were presumably present prior to elevated N deposition inputs. This critical load, which is higher than critical loads for lichens in the United States, may simply prevent further change from an already altered state. Similarly, in the Great Plains (see Chapter 11), it is not possible to determine whether the current condition of sites where deposition is lowest differs from the pristine condition (Clark and Tilman 2008). This further emphasizes the need to include “pristine” sites in gradient studies and for research experiments that remove N deposition in order to more accurately define the baseline condition, which helps describe the ecosystem state prior to elevated N deposition.

Table 19.1—Summary of empirical critical loads of nutrient N for U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

| Chapter | Ecoregion | Ecosystem Component | Critical load for N deposition <i>kg N ha⁻¹ yr⁻¹</i> | Reliability | Response | Comments | Study |
|---------|------------------|---------------------------------------|---|-------------|--|--|---|
| 5 | 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 |
| 5 | 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. | Arens et al. 2008 ^a , Hyvärinen et al. 2003 ^b , Makonen et al. 2007 ^b |
| 6 | Taiga | Lichen, moss, and algae | 1-3 | # | Changes in alga, bryophyte, and lichen community composition, cover, tissue N or growth rates. | Application of western OR and WA model for lichens | Berryman et al. 2004 ^c , Berryman and Straker 2008 ^c , Geiser et al. 2010, Moore et al. 2004 ^c , Poikolainen et al. 1998 ^b , Strengbom et al. 2003 ^d , Vitt et al. 2003 ^c |
| 6 | Taiga | Mycorrhizal fungi, spruce-fir forests | 5-7 | (#) | Ecotomycorrhizal fungi, change in community structure | Expert judgment extrapolated from Marine West coast spruce and northern spruce-fir forest | Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008 |
| 6 | Taiga | Shrublands | 6 | ## | Shrub and grass cover, increased parasitism of shrubs | Long term, low N addition study: shrub cover decreased, grass cover increased | Nordin et al. 2005 ^d , Strengbom et al. 2003 ^d |
| 7 | Northern Forests | Hardwood and coniferous forests | >3 | # | Tree growth and mortality | Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood | Thomas et al. 2010 |
| 7 | Northern Forests | Lichens | 4-6 | (#) | Epiphytic lichen community change | Loss of oligotrophic species. Synergistic/confounding effects of acidic deposition not considered; assumes response threshold similar to Marine West Coast Forests | Geiser et al. 2010 |
| 7 | Northern Forests | Ecotomycorrhizal fungi | 5-7 | # | Change in fungal community structure | | Lilleskov et al. 2008 |
| 7 | Northern Forests | Herbaceous cover species | >7 and <21 | # | Loss of prominent species | Response observed in low-level fertilization experiment | Hurd et al. 1998 |
| 7 | Northern Forests | Hardwood and coniferous forests | 8 | ## | Increased surface water NO ₃ ⁻ leaching | | Aber et al. 2003 |

| | | | | | | | |
|---|---------------------------------|-------------------------------|-------------|---------|---|---|---|
| 7 | 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 |
| 7 | Northern Forests | Arbuscular mycorrhizal fungi | <12 | (#) | Biomass decline and community composition change | As wet deposition only | van Diepen 2008, van Diepen et al. 2007 Baron 2006 |
| 8 | Northwestern Forested Mountains | Alpine lakes | 1.5 | ## | Diatom assemblages | | Baron 2006 |
| 8 | Northwestern 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 |
| 8 | Northwestern 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 |
| 8 | Northwestern Forested Mountains | Subalpine 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 | | Rueth and Baron 2002, Baron et al. 1994 |
| 8 | Northwestern Forested Mountains | Alpine lakes | 4.0 | # | Episodic freshwater acidification | | Williams and Tonneson 2000 |
| 8 | Northwestern Forested Mountains | Alpine grassland | 4-10 | ## | Plant species composition | | Bowman et al. 2006 |
| 8 | Northwestern Forested Mountains | Ectomycorrhizal fungi | 5-10 | (#) | Ectomycorrhizal fungi 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 |
| 8 | Northwestern Forested Mountains | Mixed conifer forest | 17 | ## # | NO ₃ ⁻ leaching, reduced fine root biomass | Fine root biomass in ponderosa pine is reduced by both ozone and elevated soil nitrogen | Fenn et al. 2008 |
| 9 | 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. Critical load increases with regional range in mean annual precipitation from 45-450 cm | Geiser et al. 2010 |

continued

Table 19.1—continued

| Chapter | Ecoregion | Ecosystem Component | Critical load for N deposition kg N ha ⁻¹ yr ⁻¹ | Reliability | Response | Comments | Study |
|---------|---------------------------|------------------------------|--|-------------|---|---|--|
| 9 | Marine West Coast Forests | SE Alaska forests | 5 | (#) | Fungal community change; declines in ectomycorrhizal fungal diversity | | Lilleskov 1999; Lilleskov et al. 2001, 2002; Whytemare et al. 1997 Thomas et al. 2010 |
| 10 | Eastern Temperate Forests | Eastern hardwood forest | >3 | # | Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood | | |
| 10 | Eastern Temperate Forests | Lichens | 4-8 | (#) | Epiphytic lichen community change | Loss of oligotrophic species. Synergistic/confounding effects of acidic deposition not considered. Application of western OR and WA model | Geiser et al. 2010 |
| 10 | Eastern Temperate Forests | Southeastern coastal plain | 5-10 | (#) | Ectomycorrhizal fungi community response | | Dighton et al. 2004; Lilleskov et al. 2001, 2002, 2008 |
| 10 | Eastern Temperate Forests | Eastern hardwood forests | 8 | ## | Increased surface water loading of NO ₃ ⁻ | | Aber et al. 2003 |
| 10 | Eastern Temperate Forests | Michigan deposition gradient | <12 | (#) | Arbuscular mycorrhizal fungal biomass decline and community composition change | | van Diepen 2008, van Diepen et al. 2007 |
| 10 | Eastern Temperate Forests | Herbaceous species | <17.5 | (#) | Increases in nitrophilic species, declines in species-rich genera (e.g., Viola) | | Gilliam 2006, 2007; Gilliam et al. 2006 |
| 11 | Great Plains | Tallgrass prairie | 5-15 | # | Biogeochemical N cycling, plant and insect community shifts | | Clark et al. 2009, Clark and Tilman 2008; Tilman 1993, 1987; Wedin and Tilman 1996 |
| 11 | Great Plains | Mixed-grass prairie | 10-25 | # | Soil NO ₃ ⁻ pools, leaching, plant community shifts | | Clark et al. 2003, 2005; Jorgenson et al. 2005 |
| 11 | Great Plains | Shortgrass prairie | 10-25 | (#) | | Inferred from mixed-grass prairie | Epstein 2001, Barret and Burke 2002 |
| 11 | Great Plains | Mycorrhizal fungi | 12 | (#) | Decline in arbuscular mycorrhizal fungal activity | | Egerton-Warburton ^e |

| | | | | | | | |
|----|--------------------------|---|---------|-----|---|---|--|
| 12 | North American Deserts | Lichens | 3 | (#) | Lichen community shifts, thallus N concentration | Uncertainty regarding modeled estimates | Geiser et al. 2008, Porter 2007 |
| 12 | North American Deserts | Shrubland, woodland, desert grassland | 3-8.4 | # | Vegetation response, vascular plant community change | | Allen et al. 2009; Inouye 2006; Rao et al. 2010 |
| 13 | Mediterranean California | Coastal sage scrub | 7.8-10 | # | Invasive grass cover, native forb richness, arbuscular mycorrhizal fungi richness | Modeled and inferential N deposition estimates and published data for mycorrhizae, unpublished data for vegetation survey | Allen, Egerton-Warburton and Allen 2000, Fenn et al. 2010, Tonnesen et al. 2007 |
| 13 | Mediterranean California | Chaparral; lichens | 3-6 | # | Epiphytic lichen community change | Lichen critical load is from modeled N deposition data and published data for lichens | Fenn et al. 2010, Geiser et al. 2010, Jovan 2008, Jovan and McCune 2005 |
| 13 | 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 one year of throughfall data in Chamise Creek and an additional year of throughfall data from adjacent Ash Mountain, both in Sequoia National Park | Fenn et al. 2003a, 2003b, 2003c; Fenn and Poth 1999; Meixner and Fenn 2004 |
| 13 | 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 |
| 13 | Mediterranean California | Mixed conifer forest; plant physiology | 17 | # | Reduced fine root biomass | Fine root biomass in ponderosa pine is reduced by both ozone and elevated soil nitrogen | Fenn et al. 2008, 2010; Grulke et al. 1998 |
| 13 | Mediterranean California | Mixed conifer forest; soil processes | 17-25.9 | # | NO ₃ ⁻ leaching; soil acidification | Fine root biomass in ponderosa pine is reduced by both ozone and elevated soil nitrogen | Breiner et al. 2007; Fenn et al. 2008, 2010 |
| 13 | Mediterranean California | Mixed conifer forest; forest sustainability | 24-39 | (#) | Understory biodiversity; forest sustainability | N deposition from Fenn et al. 2008 | Allen et al. 2007; Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004 |
| 13 | 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 | Fenn et al. 2010, Weiss 1999 |

continued

Table 19.1—continued

| Chapter | Ecoregion | Ecosystem Component | Critical load for N deposition <i>kg N ha⁻¹ yr⁻¹</i> | Reliability | Response | Comments | Study |
|---------|--|---|---|-------------|--|--|--|
| 15 | Temperate Sierras | Lichens | 4-7 | (#) | Epiphytic lichen community change | Increase in proportion of eutrophic species. Application of western OR and WA model, response threshold allows ~60% eutrophs due to dry, hot climate, hardwood influence | Geiser et al. 2010 |
| 15 | Temperate Sierras | Las Cruces and Chichinautzin Ranges S/SW of Mexico City | 15 | # | Elevated NO ₃ ⁻ in stream and spring waters | Data are from Mexican mountain pine (<i>Pinus hartwegii</i>) sites in the Desierto de los Leones National Park and Ajusco, Mexico | Fenn et al. 1999, 2002 |
| 16 | Tropical and Subtropical Humid Forests | N-rich forests | <5-10 | (#) | NO ₃ ⁻ leaching, N trace gas emissions | Critical load for N-rich forests should be lower than for N-poor forests based on possibility of N losses | No direct studies ⁹ |
| 16 | Tropical and Subtropical Humid Forests | N-poor forests | 5-10 | (#) | Changes in community composition; NO ₃ ⁻ leaching, N trace gas emissions | Critical load for N-poor forests based on estimates for Southeastern Coastal Plain forests | No direct studies ⁹ |
| 17 | Wetlands | Freshwater wetlands | 2.7-13 | # | Peat accumulation and net primary productivity (NPP) | Critical load for wetlands in the northeastern U.S. and southeastern Canada | Aldous 2002 ^c , Moore et al. 2004 ^c , Rochefort et al. 1990 ^c , Vitt et al. 2003 ^c |
| 17 | Wetlands | Freshwater wetlands | 6.8-14 | (#) | Pitcher plant community change | Critical load based on northeastern populations | Gotelli and Ellison 2002, 2006 |
| 17 | Wetlands | Intertidal wetlands | 50-100 | ## | Loss of eelgrass | | Latimer and Rego 2010 |
| 17 | Wetlands | Intertidal salt marshes | 63-400 | (#) | Salt marsh community structure, microbial activity and biogeochemistry | | Caffrey et al. 2007, Wigand et al. 2003 |
| 18 | Freshwaters | Western Lakes | 2 | ## | Freshwater eutrophication | | Baron 2006 |
| 18 | Freshwaters | Eastern Lakes | 8 | # | NO ₃ ⁻ leaching | | Aber et al. 2003 |

^a based on data from Greenland; ^b based on data from Finland; ^c based on data from Canada; ^d based on data from Sweden, ^e see footnote 25 on page 19-11; ^f Allen, E.B. Unpublished data. Professor and Natural Resources Extension Specialist, Department of Botany and Plant Sciences and Center for Conservation Biology, University of California, Riverside, CA 92521; ^g The critical load is based on expert judgment and knowledge of ecosystems which may function similarly.

One would expect that for an ecosystem that is nearer N saturation than another, it would take less additional N to reach a “tipping point”. However, it is important not to confuse that issue with the actual level of deposition—an ecosystem may be near N saturation when the ambient N deposition is low or when it is high. Thus, while prior exposure to elevated N deposition does push an ecosystem toward N saturation, high ambient deposition does not indicate the ecosystems most sensitive to further inputs—that status is a function of the ecosystem and the receptor.

19.7 Factors that Affect the Critical Load

One of the objectives of this assessment was to lay the groundwork for further refining and improving estimates of N critical loads. To that end, in this section, we discuss some of the factors that affect where the value of the critical load falls within the reported range (Table 19.2). We present the factors that were reported in the studies included in this report. These factors may be useful in setting empirical critical loads for specific sites as well as in the development of more complex models to assess ecosystem response to N inputs.

Abiotic factors that may affect the N critical load include elevation, latitude, topographic location, climate (temperature, precipitation, extent and rate of climate change), catchment size, soil type, extent of soil cover in high elevation systems, parent material, and hydrologic flowpaths and processes. Disturbance may also play a substantial role, for example, the type of fire regime or historical forest cutting can impact the critical load. A geographical region within the ecoregion may be more sensitive. Biological factors also likely contribute to lower N critical loads, including 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 grasses, and presence of ozone-sensitive species.

The factors discussed above may provide some guidance in applying critical loads. To set a critical load for a given site using this report, one would first determine

whether the site was similar to the site/or sites on which the critical load for that ecosystem type is based (found in the tables presented in each ecoregion chapter). If the site differs from the sites in the ecoregions tables, one would then refer to Table 19.2 to determine how to adjust the N critical load for a given site based on the range reported for the ecoregion. Finally, one would consider the general factors discussed above and adjust the critical load within the range reported for the ecoregion based on these factors.

With better identification of factors that affect the N critical load, we will move toward a mechanistic understanding of the responses and improve our ability to extrapolate observations across ecoregions or across different ecosystems within an ecoregion. In some cases, it may be possible to develop simple relationships as a function of one or several variables that would allow refinement of critical load estimates. For example, for lichens, Geiser et al. (2010) developed simple regression relationships that included precipitation volume that explain much of the variability in lichen community composition in response to N deposition. These regression models can be used to estimate N critical loads in other regions and also can provide an estimate of the uncertainty associated with the critical load.

Future research could evaluate which of these factors are most important in affecting where the critical load lies within the range for an ecoregion and determining how the critical load varies as the key parameters change across the ecoregions.

19.8 Comparison of Critical Load by Receptor across Ecoregions

Because much of the variation in critical loads occurs as a function of the receptor of concern, we compare the critical loads for the key receptors across ecoregions.

19.8.1 Mycorrhizal fungi

Background. Mycorrhizal fungi reside at the interface between host plants and soils, exchanging soil resources, especially nutrients, with host plants in exchange for photosynthates (carbon compounds). Due to this important and unique ecological niche, mycorrhizal

Table 19.2—Assessment and interpretation of empirical critical loads of nutrient N for U.S. ecoregions

| Chapter | Ecoregion | Factors affecting the range of critical loads ^a | Comparison within Ecoregion ^b |
|---------|---------------------------------|---|--|
| 5 | Tundra | moisture competition between vascular plants and cryptogams P-limitation temperature pH | The critical load is 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. |
| 6 | Taiga | soil depth vegetation type and species composition latitude | Morphological damage to lichens has been observed at a lower deposition in forests and woodlands than in shrublands or bogs and fens; cryptogam dominated mats on thin soils become N saturated faster than forest islands. |
| 7 | Northern Forests | receptor tree species stand age site history pre-existing N status | Critical loads for lichens are generally lowest, followed by critical loads for ectomycorrhizal fungi and NO_3^- leaching. Critical loads for herbaceous species and forests are generally higher than for other responses. |
| 8 | Northwestern Forested Mountains | biotic receptor accumulated load of N ecosystem region | In alpine regions, diatom changes in lakes are seen at the lowest critical load. Changes in individual plants are seen next, followed by vegetation community change, then soil responses. In subalpine forests, the critical load of $4 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for foliar and soil chemistry changes is similar to the lichen critical load of $3.1 - 5.2$ for lichen community change. |
| 9 | Marine West Coast Forests | background N status soil type species composition fire history climate | The midrange of responses reported for lichens ($2.7 - 9.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$) is broadly comparable to that for plant, soil, and mycorrhizal responses ($5 \text{ kg ha}^{-1} \text{ yr}^{-1}$), despite limited studies for non-lichen responses. |
| 10 | Eastern Forests | precipitation soil cation fertility and weathering biotic receptors | The critical load for NO_3^- leaching, lichen community change, and ectomycorrhizal fungal response are within the same range. Arbuscular mycorrhizal fungal and herbaceous critical loads are higher. |
| 11 | Great Plains | N status receptor precipitation | Critical loads are lower in the tall grass prairie than in the mixed- and short-grass prairies. Critical loads in tall- and mixed-grass prairie is lower on N poor sites and sites with very N responsive plant species. Critical loads in the short-grass prairie is likely lower in wet years than in dry years. |

| | | | |
|----|--------------------------|--|--|
| 12 | North American Deserts | receptor interaction of annual grasses with native forb cover precipitation | The lichen critical load is lowest, at 3 kg N ha ⁻¹ yr ⁻¹ ; vegetation critical load varies from 3 to 8.4 kg N ha ⁻¹ yr ⁻¹ |
| 13 | Mediterranean California | presence of invasive exotic annual grasses interacting with a highly diverse native forb community N-sensitivity of mycorrhizal fungi N-sensitivity of lichens N retention capacity of catchments, catchment size co-occurrence of ozone and ozone-sensitive tree species. | The lowest critical loads in Mediterranean California are for sensitive lichen in chaparral and oak woodlands and mixed conifer forests. The critical load for plant and mycorrhizal fungal community change in coastal sage scrub is higher, at 7.8 to 10 kg ha ⁻¹ yr ⁻¹ . Critical load for NO ₃ ⁻ leaching is lower in chaparral and oak woodlands (10 to 14 kg ha ⁻¹ yr ⁻¹) than in mixed conifer forests (17 kg ha ⁻¹ yr ⁻¹). Critical loads are highest for mixed conifer forest plant community change and sustainability. |
| 17 | Wetlands | vegetation species fraction of rainfall in the total water budget degree of openness of N cycling | Critical load is much higher for intertidal wetlands (50 to 400 kg ha ⁻¹ y ⁻¹) than for freshwater wetlands (2.7 to 14 kg ha ⁻¹ y ⁻¹), which have relatively closed water and N cycles. |

^aThis explains what factors cause the critical load (CL) to be at the low or high end of the range reported.

^bComparison of values and causes for differences if multiple critical loads are reported for an ecoregion.

fungi are at particular risk due to changes in either the soil environment or host carbon allocation.

Response to N inputs. Nitrogen deposition adversely affects mycorrhizal fungi primarily in two ways: (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 that are 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 in this report, mycorrhizal fungi appear to be less sensitive to N deposition than lichens (Tables 19.3 and 19.4), presumably because the soil environment buffers these soil fungi from some of the immediate impacts of N deposition, whereas lichens are directly exposed to atmospheric N pollution. (Lichens have an advantage as indicators when compared with mycorrhizal fungi because they can be relatively easily inventoried.) However, the essential role of mycorrhizal fungi as root symbionts central to plant nutrition and belowground production, as repositories of a large part of the eukaryote diversity in forests, as major components of forest food webs, and as nontimber forest products of high economic value (edible sporocarps) (Amaranthus 1998) provides sufficient justification to improve our understanding of their response to N deposition.

Critical loads of N for mycorrhizal fungi. We reviewed empirical studies on mycorrhizal fungal response to N inputs as the basis for determining empirical critical

loads for the United States (Table 19.3, Figure 19.1). Despite the sparse data, it is clear that N deposition sufficient to elevate inorganic N, and 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 to 10 $\text{kg ha}^{-1} \text{yr}^{-1}$ 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 N deposition levels of 7.8 to 12 $\text{kg ha}^{-1} \text{yr}^{-1}$ can lead to community changes, declines in spore abundance and root colonization, and changes in community function, based on reanalysis of data from Egerton-Warburton et al. (2000) combined with N deposition data and decreases in fungal abundance (van Diepen et al. 2007, Van Diepen 2008) and declines in fungal activity.²⁴ 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, our provisional expert judgment is that critical loads for mycorrhizal diversity for sensitive ecosystem types are 5 to 10 $\text{kg ha}^{-1} \text{yr}^{-1}$. There is high uncertainty in this estimate because few studies have been conducted at low N deposition to further refine the critical load.

The critical load of N for mycorrhizal fungi, when community change occurs, is often on the order of current N deposition and thus is exceeded across much of the Eastern Temperate and Northern Forests ecoregions. Exceedance of N critical loads is more variable in the western United States. The critical load is exceeded in regions downwind of agricultural and urban emissions in the West (Figure 19.2). In the Northwestern Forested Mountains and Marine West Coast Forests, N deposition is generally below the critical load, although the lower end of the critical load range is exceeded in the Cascade Mountains. A similar pattern can be seen in Mediterranean California; the N critical load for mycorrhizal fungi is exceeded in the vicinity of the Sierra Nevada and in the

²⁴ Egerton-Warburton, L.M. Unpublished data. Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL, 60022

Table 19.3—Empirical critical loads of nutrient N for mycorrhizal fungi in U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

| Ecoregion | Ecosystem (Site) | Critical load for N deposition <i>kg ha⁻¹ yr⁻¹</i> | Reliability | Response | Comments | Study |
|---------------------------------|--|---|-------------|---|---|--|
| Taiga | Spruce forests | 5-7 | (#) | Ectomycorrhizal fungi, change in community structure | Expert judgment extrapolated from Marine West Coast spruce and northern spruce-fir forest | Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008 |
| Northern Forests | Spruce-fir forest (Northeastern U.S. deposition gradient) | 5-7 | # | Ectomycorrhizal fungi, change in community structure | Wet deposition estimated from Ollinger et al. (1993) model | Lilleskov et al. 2008 |
| Northern Forests | Northern hardwood forests; sugar maple dominated (Michigan gradient) | <12 | (#) | Arbuscular mycorrhizal fungi, decrease in abundance in roots, soil, community change | N fertilization experiment | van Diepen et al. 2007, van Diepen 2008 |
| Northwestern Forested Mountains | Engelmann spruce forests | 5-10 | (#) | Ectomycorrhizal fungi, change in community structure | Expert judgment extrapolated from Marine West coast spruce and northern spruce-fir forest | Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008 |
| Marine West Coast Forests | White spruce forest (Kenai Peninsula, Alaska) | 5 | (#) | Ectomycorrhizal fungi, change in community structure, decrease in species richness | Bulk deposition. Historic N deposition was higher but not quantified. Critical load estimated from regression | Lilleskov 1999, Lilleskov et al. 2001, 2002, Whytemare et al. 1997 |
| Eastern Temperate Forests | Southeastern Coastal Plain | 5-10 | (#) | Ectomycorrhizal fungi, change in community structure | From one study in pine barrens plus extrapolation from other oligotrophic conifer forests | Dighton et al. 2004; Lilleskov et al. 2001, 2002, 2008 |
| Eastern Temperate Forests | Pine Barrens (New Jersey; Southeastern Coastal Plain) | <8 | (#) | Ectomycorrhizal fungal morphotype community change | Bulk deposition. Gradient study with three sample points | Dighton et al. 2004 |
| Eastern Temperate Forests | Eastern hardwoods; sugar maple dominated (Michigan gradient) | <12 | (#) | Arbuscular mycorrhizal fungi; decrease in abundance in roots, soil, community change | Long-term (12 yr) N fertilization experiment in sugar maple | van Diepen et al. 2007, van Diepen 2008 |
| Great Plains | Chicago grassland | 12 | (#) | Arbuscular mycorrhizal fungi; decrease in % colonization, spore density | Critical load estimated from logarithmic curve of soil N vs. arbuscular mycorrhizal fungal activity. No low N baseline, so critical load may be lower | Egerton-Warburton ^a |
| Mediterranean California | Coastal sage scrub (southern California) | 7.8-9.2 | # | Arbuscular mycorrhizal fungi, decrease in % colonization, spore density, spore richness | Critical load estimated from logarithmic curve fitted to data from this study compared to modeled and inferential N deposition data | Egerton-Warburton and Allen 2000, Fenn et al. 2010, Tonnesen et al. 2007 |

^asee footnote 24 on page 244

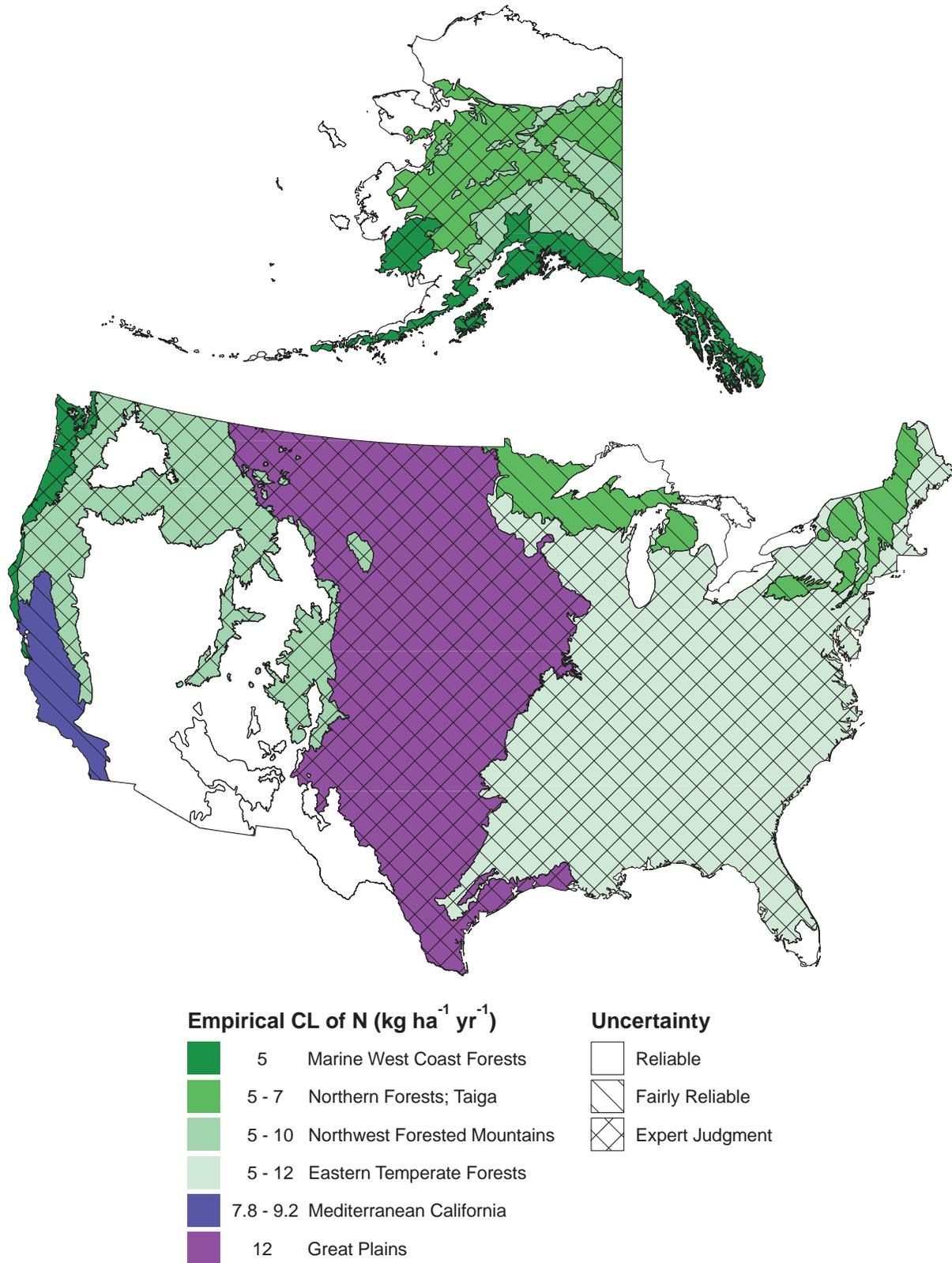


Figure 19.1—Map of critical loads (CL) for mycorrhizal fungi by ecoregion in the United States. The range of critical loads reported for mycorrhizal fungi is shown for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain “reliable” category, single hatching for the “fairly reliable” category, and double hatching for the “expert judgment” category. The color 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 color decreases. White areas lack data for critical loads determination for mycorrhizal fungi.

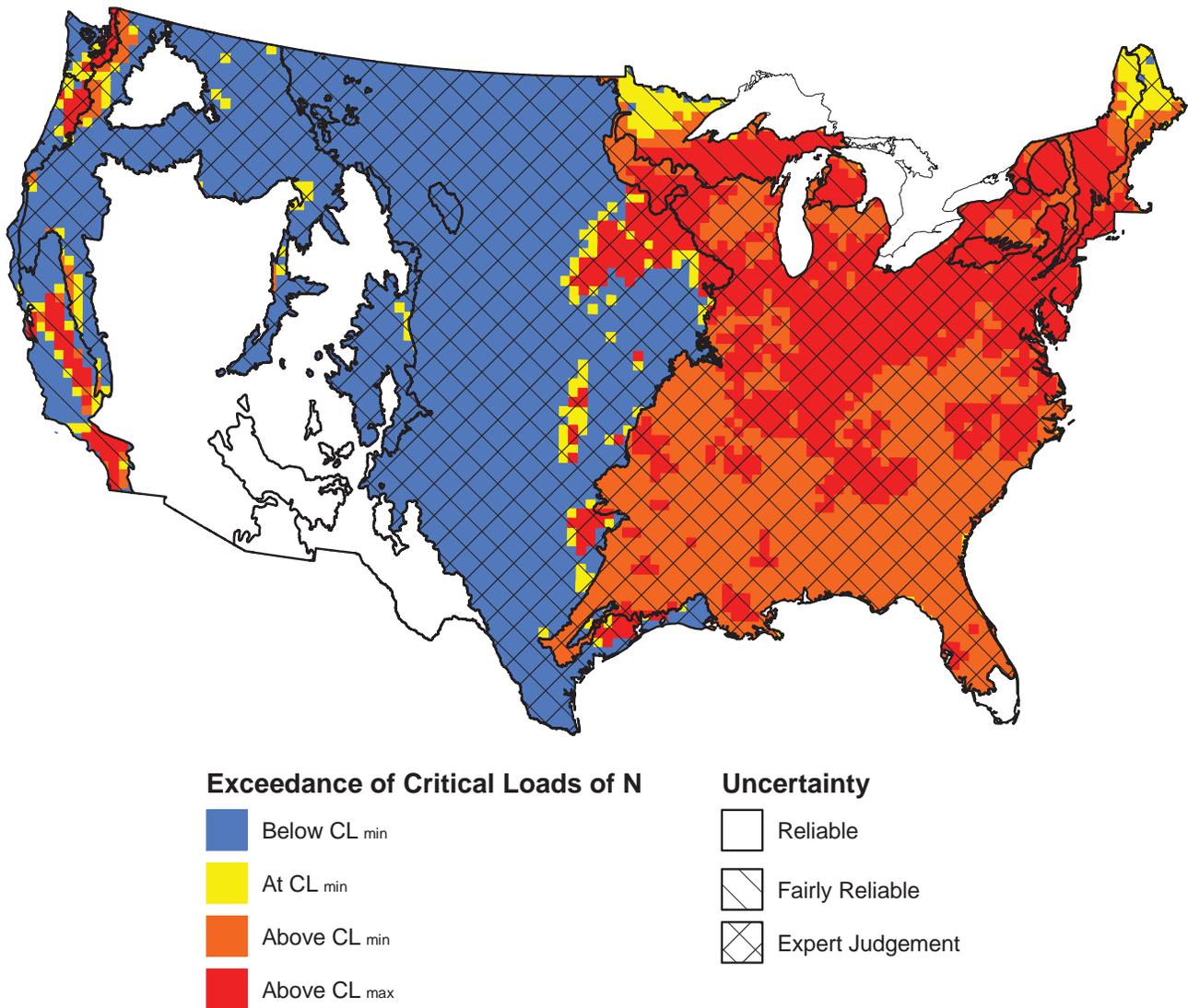


Figure 19.2—Map of exceedance of critical loads (CL) for mycorrhizal fungi by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load - deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for mycorrhizal fungi.

Transverse Mountain ranges of southern California. The uncertainty associated with the exceedance, like that for the critical load, is high.

19.8.2 Lichens and Bryophytes

Background. Lichens and bryophytes make substantial contributions to biodiversity. About 4100 lichen and 2300 bryophyte species are known from North America north of Mexico—as about one-fourth of vascular plant diversity, which is about 26,600 species (NRCS 2009). Therefore, N critical loads protective of the sensitive

lichens and bryophytes help protect biological diversity. Lichens are symbiotic organisms consisting of a fungus, for which the organism is named, and a green algal and/or a blue-green bacterial partner. Bryophytes are small, thin-leaved, nonvascular plants encompassing the mosses, liverworts, and hornworts. Neither lichens nor bryophytes have true roots or other specialized conductive tissues. Individual species are adapted to specific nutrient availability regimes, therefore oligotrophic environments will be characterized by different species than eutrophic environments.

Responses to N inputs. 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. 2003a, 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 quickly dehydrate to a metabolically inactive state 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 to much of the broader forest ecosystem (McCune et al. 2007). In some cases, alteration of lichen community composition may signal the beginning of a cascade of changes in ecosystem N cycling, which may markedly alter the structure or function of the ecosystem as a whole. In many cases, changes in lichens may have implications in portions of the ecosystem beyond the lichen community. In other cases, alterations in the lichen community may have little impact on the overall structure and function of the ecosystem. It can be difficult to know at the outset whether the ultimate consequences of changes indicated by alterations to the lichen community will be large or small for the overall ecosystem over the long term.

Lichens and bryophytes can play important roles in ecosystems. 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 eutrophic (i.e., nitrogen 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, lichens and bryophytes, together with other microbiota, form cryptogamic mats important to soil stabilization and fertility.

A hypothetical example of sensitive species diminishing to the extent where they cannot fulfill their ecological roles for the northern flying squirrel of Pacific Northwest forests follows. Over 90 percent of the squirrel's diet consists of hypogeous and epigeous mycorrhizal fungi in summer and the N-sensitive horsehair lichen (*Bryoria fremontii*) in winter. The squirrel is both an important dispersal agent for mycorrhizal fungi (obligate symbionts with the roots of conifer trees) and a primary prey of the northern spotted owl (*Strix occidentalis*), a threatened and endangered species (Maser et al. 1985). If N deposition extirpated the horsehair lichen, as it nearly has in the Netherlands (van Herk et al. 2003), all dependent species would presumably decline regardless of whether they are themselves sensitive to N deposition.

Critical loads of N for lichens. The N critical loads estimated in this report for lichens range from 1 to 9 kg N ha⁻¹ yr⁻¹ (Table 19.4, Figure 19.3). Although the reported range of N critical loads is not as large as the ranges for forests or herbs, the certainty associated with these estimates varies considerably. This is partially because of differences in sampling scheme and intensity. For example in the Pacific Northwest and California, lichen communities were assessed intensively across wide environmental gradients spanning low to high N deposition on a fine grid over time (Geiser and Neitlich 2007, Jovan 2008), yielding highly reliable critical N load estimates. Assessments in the eastern United States are more problematic, due to historical and contemporary S emissions and acid deposition. In such cases, where historical information necessary to identify a "pristine" or "clean" state is lacking, it is more difficult to determine the N critical load, and the resulting confidence associated with the critical load is low. The critical load of N for lichens, based on the shift

in community composition when eutrophs dominate at the expense of oligotrophs, is on the order of current N deposition and thus is exceeded across much of the Eastern Temperate and Northern Forest ecoregions and in many areas (e.g., high deposition) in the West (Figure 19.4). The uncertainty associated with the exceedance, like that for the critical load, is low for the Marine West Coast and Northwestern Forested Mountains ecoregions and Mediterranean California forests, but high elsewhere.

Studies in the Pacific Northwest demonstrate that increasing precipitation allows lichens to tolerate higher N deposition (Geiser and Neitlich 2007, Geiser et al. 2010, Chapter 4). The importance of precipitation volume in the N critical load for lichens is likely due to the direct influence of N concentration on lichens, that is, the concentrations of N compounds to which lichens are exposed are more important than total N loading (Geiser et al. 2010). 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.

19.8.3 Herbaceous Species and Shrubs

Background. Herbaceous species and shrubs (Table 19.5, Figure 19.5) 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 (NRCS 2009).

Response to N inputs. Herbaceous species and some shrubs appear intermediate between cryptogram 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 cryptograms, 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 species in alpine or tundra environments will respond later and to a lesser degree than the cryptograms with which they coexist. Herbaceous plants obviously 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 has an importance that is disproportionate to its relatively low biomass. For example, although they represent only approximately 0.2 percent of standing aboveground biomass, herbaceous understory species produce more than 15 percent of forest litter biomass and comprise up to 90 percent of forest plant biodiversity, including endangered or threatened species (Gilliam 2007).

Critical loads of N for herbaceous vegetation. The range of critical loads for N for herbaceous species and shrubs across all ecoregions is 3 to 33 kg N ha⁻¹ yr⁻¹ (Table 19.5, Figure 19.5). Although this range is broader than those for lichens or mycorrhizal fungi, many of the critical loads for herbaceous species fall into the range of 5 to 15 kg N ha⁻¹ yr⁻¹. There is moderate uncertainty in these estimates. The shorter lifespan of some herbaceous species results in a more rapid response to N addition. This pattern is especially relevant for annuals and perennials with little N storage. In grasslands, for example, elevated N deposition often leads to a rapid (1 to 10 years) increase in herbaceous production and a shift in biomass allocation towards more aboveground 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). Experimental studies of moderate to long duration (3 to 10 years) allow determination of the N 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 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, Adams et al. (2006) added 35 kg N ha⁻¹ yr⁻¹ via aerial N application in addition to ambient deposition of 15 to 20 kg N ha⁻¹ yr⁻¹, which has led to changes in understory species composition. Recently, similar changes in understory species composition have occurred on the adjacent reference watershed receiving

Table 19.4—Empirical critical loads of nutrient N for lichens in U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; # expert judgment

| Ecoregion | Ecosystem (Site) | Critical load for N deposition $kg\ ha^{-1}\ yr^{-1}$ | Reliability | Response of | Comments | Study |
|------------------------------|---|--|-------------|---|--|---|
| Tundra | Tundra | 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 | Arens et al. 2008 ^a , Hyvärinen et al. 2003 ^b , Makkonen et al. 2007 ^b |
| Taiga | Taiga | 1-3 | # | Changes in alga, bryophyte, and lichen community composition, cover, tissue N or growth rates | | Berryman et al. 2004 ^c , Berryman and Straker 2008 ^c , Geiser et al. 2010, Moore et al. 2004 ^c , Poikolainen et al. 1998 ^b , Strengbom et al. 2003 ^d , Vitt et al. 2003 ^c |
| Northern Forests | Northern Forests | 4-6 | (#) | Changes in lichen physiology and community structure | Application of western OR and WA model | Geiser et al. 2010 |
| Northwest Forested Mountains | Coniferous forests, Alaska | 1.2-3.7 | (#) | Lichen community composition change | Application of western OR and WA model | Geiser et al. 2010 |
| Northwest Forested Mountains | Coniferous Forests, non- Alaska | 2.5-7.1 | ## | Lichen community composition change | Application of western OR and WA model | Geiser et al. 2010 |
| Northwest Forested Mountains | Central Southern Sierras | 3.1-5.2 | ## | Shifts in epiphytic lichen communities favoring eutrophs | Critical load based on exceedance of a N concentration threshold in the lichen <i>Letharia vulpina</i> | Fenn et al. 2008, 2010 |
| Marine West Coast Forests | Western OR and WA forests | 2.7-9.2 | ## | Shifts in epiphytic lichen communities favoring eutrophs | Critical load increases with increasing mean annual precipitation from 40 to 240 cm | Geiser et al. 2010 |
| Eastern Forests | Eastern hardwoods and Southeast Coastal Plain | 4-8 4-6 | (#) (#) | Shifts in epiphytic lichen communities favoring eutrophs | Application of western OR and WA model | Geiser et al. 2010 |
| North American Deserts | Cold desert (Hells Canyon National Resource Area) | 3 | (#) | Increased cover and abundance of nitrophilous lichens on tall shrubs, increased parasitism of lichens | Critical load estimated from overlay of course grid (36 km) CMAQ N; local N deposition from NH_3 was likely higher | Geiser et al. 2008, Porter 2007 |

| | | | | | | |
|--------------------------|---|---------|-----|--|---|---|
| Mediterranean California | Oak woodlands and chaparral (Central Valley, Coast Ranges and Sierra foothills) | 3-6 | # | Shifts in epiphytic lichen communities favoring eutrophs | Forest Health Monitoring (FHM) lichen survey of 118 forested sites. Eutrophs dominated communities when CMAQ 4 km N deposition estimates were >5.5 kg ha ⁻¹ yr ⁻¹ | Fenn et al. 2010, Geiser et al. 2010, Jovan 2008, Jovan and McCune 2005 |
| Mediterranean California | Mixed Conifer forest (Sierra Nevada) | 3.1-5.2 | ## | Shifts in epiphytic lichen communities favoring eutrophs | Extrapolated from Northwestern Forested Mountains Sierra Nevada study | Fenn et al. 2008, 2010 |
| Temperate Sierras | Lichens | 4-7 | (#) | Shifts in epiphytic lichen communities favoring eutrophs | Application of western OR and WA model | Geiser et al. 2010 |

^a based on data from Greenland; ^b based on data from Finland; ^c based on data from Canada; ^d based on data from Sweden

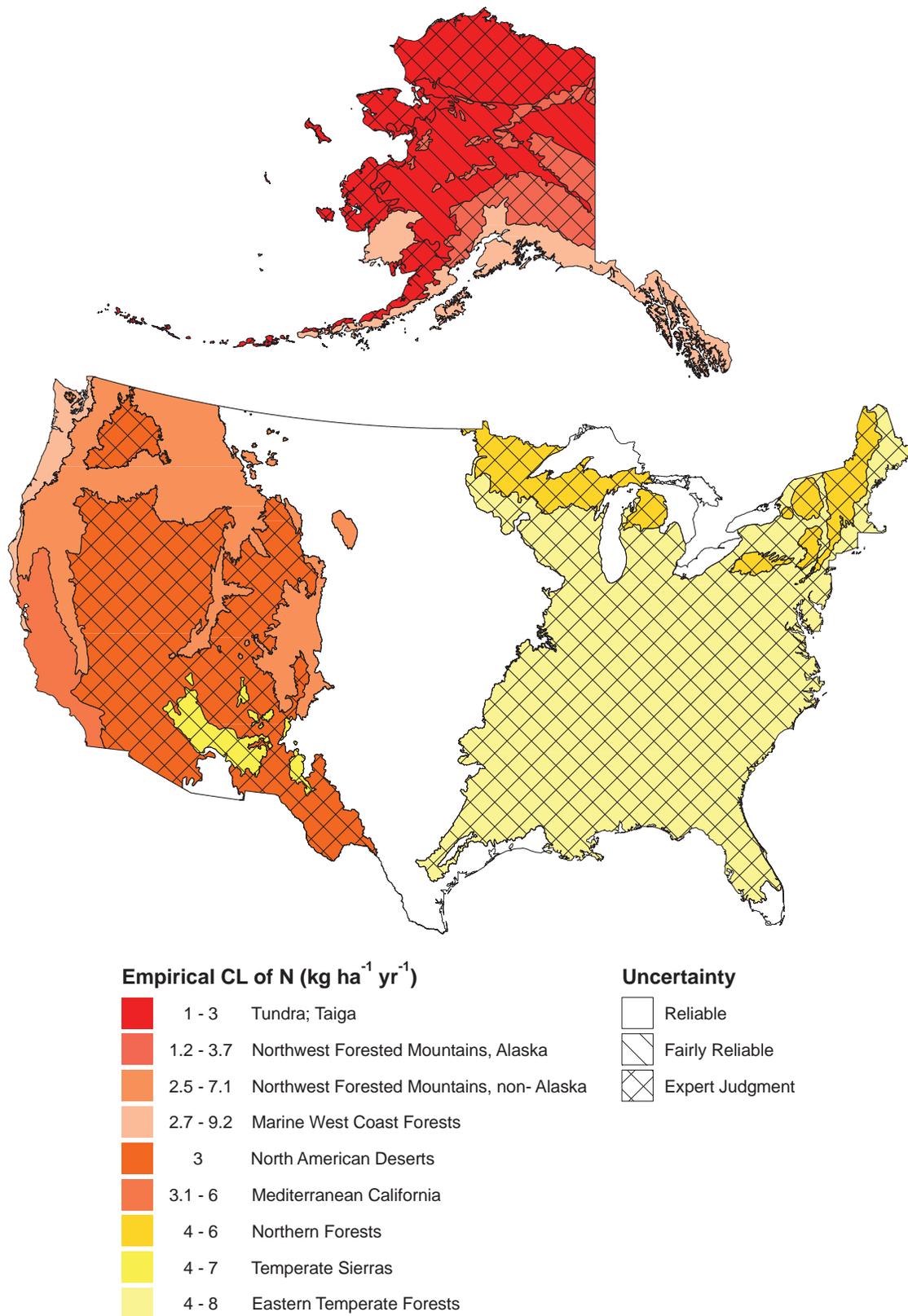


Figure 19.3—Map of critical loads (CL) for lichens by ecoregion in the United States. The range of critical loads reported for lichens is shown for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain “reliable” category, single hatching for the “fairly reliable” category, and double hatching for the “expert judgment” category. The color 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 color decreases. White areas lack data for critical loads determination for lichens.

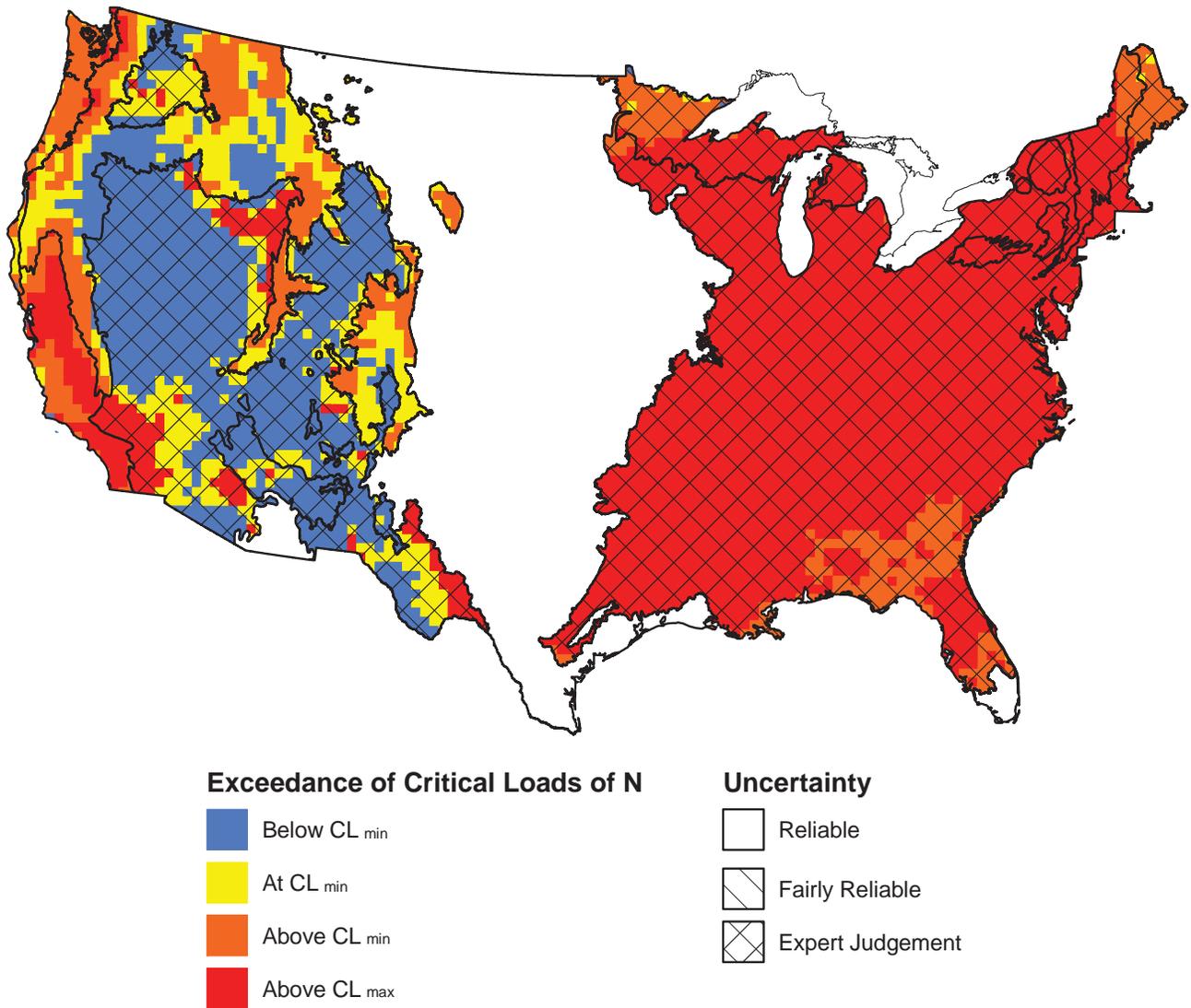


Figure 19.4—Map of exceedance of critical loads (CL) for lichen by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load - deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for lichens.

only ambient atmospheric deposition (Gilliam et al. 1996).²⁵ This pattern suggests that N deposition to the reference watershed currently exceeds the critical load. It is difficult to determine the empirical N critical load at sites where ambient deposition exceeds the critical load. Where deposition rates exceed the critical load, empirical measurement of the rate of change of an ecological metric (e.g., plant abundance, diversity, or community composition) over a range of N inputs

²⁵Gilliam, F.S. Unpublished data. Professor, Department of Biological Sciences, Marshall University, Huntington, WV 25755-2510.

provides an approach to estimate the N level at which that metric begins to change (Bowman et al. 2006).

The critical load of N for herbaceous species and herbs, when community change occurs (in some cases with exotic invasives replacing native species), is exceeded across much of the Great Plains ecoregion, in portions of the Southwest, and in high elevation and high deposition areas of the other ecoregions (Figure 19.6). The uncertainty associated with the exceedance, like that for the critical load, varies.

Table 19.5—Empirical critical loads of nutrient N for herbaceous plants and shrubs in U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

| Ecoregion | Ecosystem (Site) | Critical load for N <i>kg ha⁻¹ yr⁻¹</i> | Reliability | Response | Comments | Study |
|---------------------------------|---|--|-------------|--|---|--|
| Tundra | Prostrate dwarf shrub | 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 |
| 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 | Nordin et al. 2005 ^b , Strengbom et al. 2003 ^b |
| Northern Forests | Northern hardwood forests (Adirondacks) | >7 and <21 | # | Alteration of herbaceous understory | | Hurd et al. 1998 |
| Northwestern Forested Mountains | Alpine grasslands | 4-10 | ## | Plant species composition change | Based on long-term experiment | Bowman et al. 2006 |
| Eastern Forests | Eastern hardwood forests (Fernow Experimental Forest, WV) | <17.5 | (#) | Increases in nitrophilic species, declines in species-rich genera (e.g., <i>Viola</i>) | | Gilliam 2006, Gilliam 2007, Gilliam et al. 2006 |
| Great Plains | Tallgrass prairie | 5-15 | # | Biogeochemical N cycling, plant and insect community shifts | Long-term, low N addition study that also added other nutrients. | Clark et al. 2009; Clark and Tilman 2008; Tilman 1993, 1987; Wedin and Tilman 1996 |
| Great Plains | Mixed-grass prairie | 10-25 | # | Soil NO ₃ ⁻ pools, leaching, plant community shifts | Short-term, low N addition study | Jorgenson et al. 2005, Clark et al. 2003, 2005 |
| Great Plains | Shortgrass prairie | 10-25 | (#) | | Inferred from mixed-grass prairie | Epstein 2001, Barrett and Burke 2002 |
| North American Desert | Warm desert (Joshua Tree National Park, Mojave Desert) | 3-8.4 | # | Increased biomass of invasive grasses; decrease of native forbs | | Allen et al. 2009; Inouye 2006; Rao et al. 2009, 2010 |

| | | | | | | |
|--------------------------|--|--------|-----|--|--|--|
| 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 | Fenn et al. 2010, Weiss 1999 |
| Mediterranean California | Coastal sage scrub | 7.8-10 | # | Invasive grass cover, native forb richness | Modeled and inferential N deposition estimates and unpublished data for vegetation survey | Allen unpublished ^c , Egerton-Warburton et al. 2001, Fenn et al. 2010, Tonnesen et al. 2007 |
| Mediterranean California | Mixed conifer forests (San Bernardino Mountains) | 24-33 | (#) | Biodiversity of understory: percent cover and no. of species/3 ha | Based on plant surveys in 1970s and 2003 | Allen et al. 2007 N deposition data: Fenn et al. 2008 and Fenn ^d |
| Wetlands | Freshwater wetlands | 6.8-14 | (#) | Pitcher plant community change | Critical load based on northeastern populations | Gotelli and Ellison 2002, Latimer and Rego 2010 |
| Wetlands | Intertidal wetlands | 50-100 | ## | Loss of eelgrass | | |
| Wetlands | Intertidal salt marsh | 63-400 | (#) | Salt marsh community structure, microbial activity and biogeochemistry | | Caffrey et al. 2007, Wigand et al. 2003 |

^a based on data from Greenland; ^b based on data from Sweden; ^c Allen, E.B. Unpublished data. Professor and Natural Resources Extension Specialist, Department of Botany and Plant Sciences and Center for Conservation Biology, University of California, Riverside, CA 92521; ^d Fenn, M.E. Unpublished data. Research plant pathologist, Forest Fire Laboratory, 4955 Canyon Crest Dr., Riverside, CA 92507.

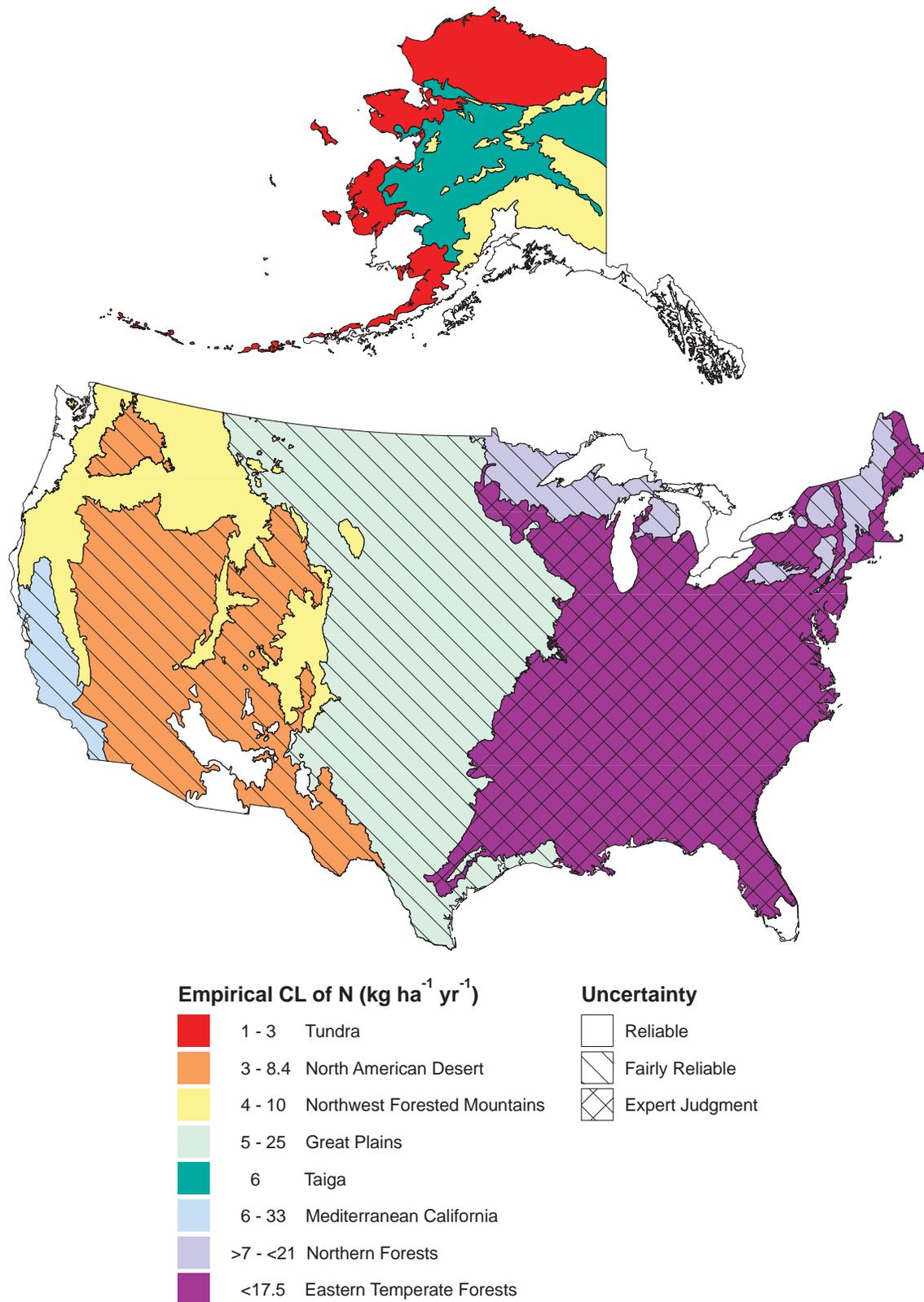


Figure 19.5—Map of critical loads (CL) for herbaceous plants and shrubs by ecoregion in the United States. The range of critical loads reported for herbaceous plants and shrubs is shown for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain “reliable” category, single hatching for the “fairly reliable” category, and double hatching for the “expert judgment” category. The color 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 color decreases. White areas lack data for critical loads determination for herbaceous species and shrubs.

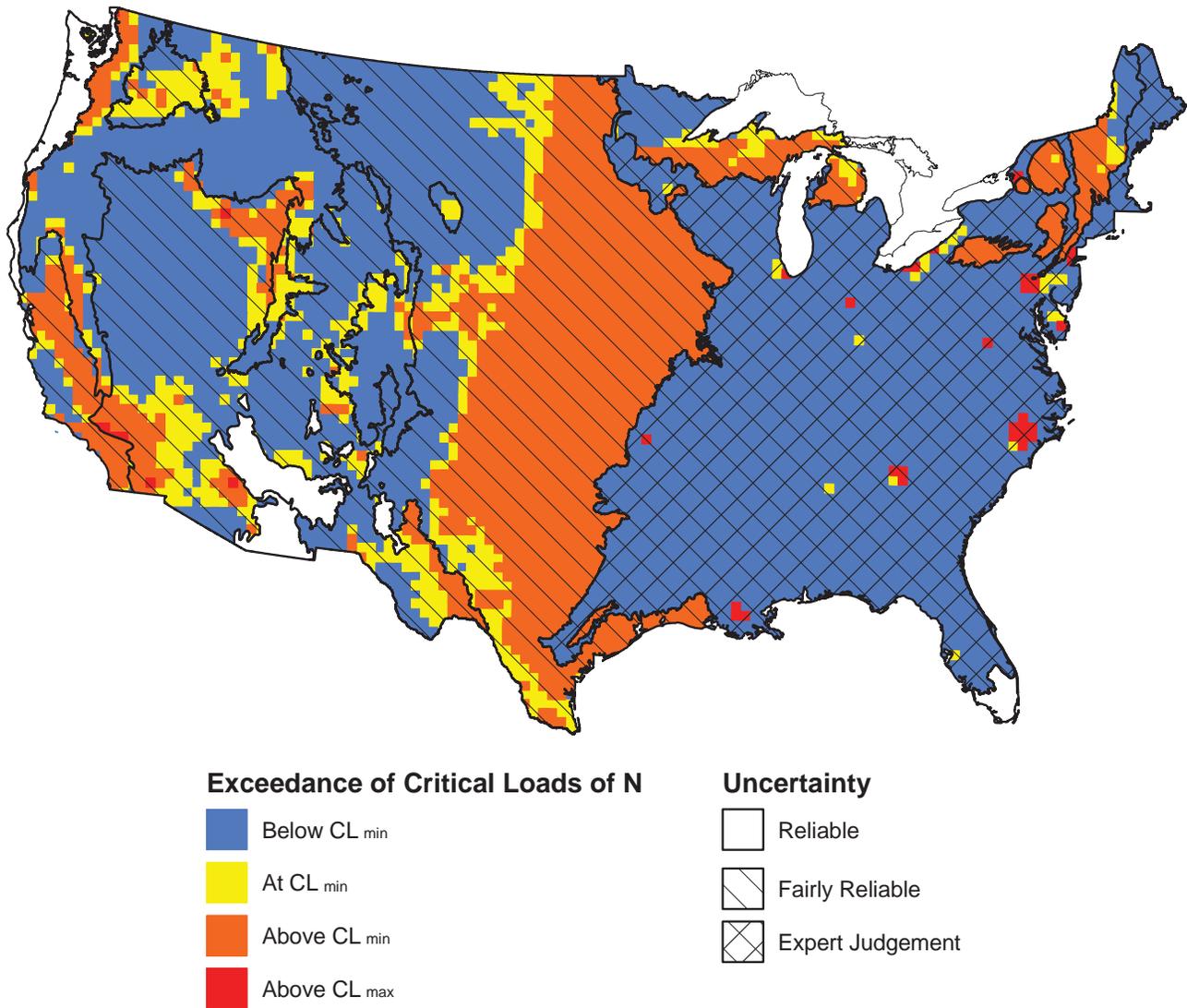


Figure 19.6—Map of exceedance of critical loads (CL) for herbaceous plants and shrubs by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load - deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min} , when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max} , when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for herbaceous species and shrubs.

Comparisons of N critical load with current deposition indicates that the low end of the critical load range for herbaceous species is exceeded for most of the Great Plains and Mediterranean California ecoregions (Figure 19.6). The low end of the critical load range is also exceeded in portions of the Eastern Temperate Forests, Northern Forests, Northeastern Forested Mountains, and North American Deserts ecoregions; uncertainty for exceedance varies. Portions of the Cascade Mountain range, the Rocky Mountains, the Adirondacks, and the

Green and White Mountain ranges exceed the low end of the critical load range.

19.8.4 Trees/Forest Ecosystems

Background. In this section we discuss the responses of trees and the biogeochemical responses of forest ecosystems to N inputs (Table 19.6), excluding the specific responses of mycorrhizal fungi, lichens, or understory herbaceous plants. Forest ecosystems represent a third of landcover in the United States

(USFS 2001) and are significant in the Northern, Eastern Temperate, Tropical and Subtropical Humid, and Marine West Coast Forests; Northwestern Forest Mountains; and Mediterranean California ecoregions.

Response to N inputs. In northeastern forests, gradient studies demonstrate that N deposition enhances growth in some fast-growing tree species, including the hardwoods studied with arbuscular mycorrhizal associations, whereas it slows growth in some species (red spruce, red maple [*Acer rubrum*]), and has no detectable effect on still other species (Thomas et al. 2010). Similarly, N deposition enhances survivorship in a few species (black cherry [*Prunus serotina*], red maple, paper birch [*Betula papyrifera*]) and decreases survivorship in others (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 because of the long response time of trees and forest soils to changes in N inputs and N availability (Table 19.6). The relatively large pools of organic N in the forest floor, mineral soil, tree biomass, and detritus contribute to the relatively long lag time in forest ecosystem response to N inputs. Because of the long lag time in response to N treatments, it can be difficult to determine the actual critical N load 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 N critical load, in part because large N storage pools give forest ecosystems a greater capacity to buffer N inputs. In

herbaceous plants, too, responses in individual species tend to be observed at lower N inputs than changes in community composition, which are more complex and interconnected (Bowman et al. 2006).

Critical loads of N in forests. The range of critical loads reported for forest ecosystems is 4 to 39 kg N ha⁻¹ yr⁻¹ (Table 19.6, Figure 19.7). The threshold N deposition value which caused increased NO₃⁻ leaching from forest ecosystems into surface water was 8 to 17 kg N ha⁻¹ yr⁻¹; the lower end of the range represents Northern and Eastern Temperate Forests, the upper end represents Mediterranean California mixed conifers (Table 19.6, Figure 19.7). At 4 kg N ha⁻¹ yr⁻¹, increasing [NO₃⁻] was reported in the organic horizon in the Colorado Front Range, which suggests incipient N saturation (Rueth and Baron 2002). The highest critical loads were reported for Mediterranean California mixed-conifer forests for soil acidification caused by increased N deposition and for forest sustainability. These sites experience some of the highest N deposition reported in the United States, up to approximately 70 kg N ha⁻¹ yr⁻¹ (Fenn et al. 2008).

The N critical load is exceeded across much of the eastern forests (Eastern Temperate and Northern Forest ecoregions). The lower end of the N critical load range is exceeded for the remaining portions of the eastern forests, as well as portions of the Marine West Coast, Northwestern Forested Mountains, and Tropical and Subtropical Humid Forest ecoregions (Figure 19.8). The N critical load for forest ecosystems was not exceeded for much of area of the Mediterranean California ecoregion, in part because the critical load was very high and, in part, because the CMAQ 2001 deposition that we used was at a coarse resolution that underestimates deposition compared to the finer scale (4 km x 4 km grid) used by Fenn et al. (2010). The critical load for nitrate leaching (Figure 19.9) is exceeded in portions of the Mediterranean California and the lower end of the critical load range is exceeded for most eastern forest and part of the Great Plains (Figure 19.10).

19.8.5 Inland Surface Waters and Wetland Ecosystems

Background. Freshwater lakes and streams, and wetlands (freshwater and estuarine intertidal) are ecosystem

Table 19.6—Empirical critical loads of nutrient N for forest ecosystems in U.S. ecoregions. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

| Ecoregion | Ecosystem (Site) | CL for N <i>kg ha⁻¹ yr⁻¹</i> | Reliability | Response | Comments | Study |
|---------------------------------|---|---|-------------|--|---|--|
| Northern Forests | Northeastern gradient | >3 | # | Decline in survivorship of sensitive species | Based on study of gradient of N deposition from 3-11 kg N ha ⁻¹ yr ⁻¹ | Thomas et al. 2010 |
| Northern Forests | Hardwood and coniferous forests | 8 | ## | Increased surface water and NO ₃ ⁻ leaching | | Aber et al. 2003 |
| Northern Forests | Montane spruce fir (Mt. Ascutney, VT) | >10 and <26 | # | Declines in growth and increased mortality | | McNulty et al. 2005 |
| Northwestern Forested Mountains | Subalpine forest | 4 | ## | soil organic horizon and foliar N enrichment and higher potential net N mineralization rates | | Baron et al. 1994, Rueth and Baron 2002 |
| Northwestern Forested Mountains | Mixed conifer forest | 17 | ## # | NO ₃ ⁻ leaching, reduced fine root biomass | Co-occurring ozone also affects fine root biomass in ponderosa pine | Fenn et al. 2008 |
| Marine West Coast Forests | Coastal white spruce forest (South-Central Alaska) | 5 | (#) | Declines in tree health; changes in understory composition; foliar nutrient imbalances; elevated NO ₃ ⁻ in forest floor and mineral soil | | Lilleskov 1999, Lilleskov et al. 2001, 2002; Whytemare et al. 1997 |
| Eastern Forests | Eastern hardwood forests | >3 | # | Decline in survivorship of sensitive species | Based on study of gradient of N deposition from 3-11 kg N ha ⁻¹ yr ⁻¹ | Thomas et al. 2010 |
| Eastern Forests | Eastern Hardwood Forests | 8 | ## | Increased surface water loading of NO ₃ ⁻ | | Aber et al. 2003 |
| Mediterranean California | Mixed conifer forests (San Bernardino Mountains and southern Sierra Nevada range) | 17 | ## | Streamwater [NO ₃ ⁻] > 14 μM | Based on regression of throughfall vs. peak streamwater NO ₃ ⁻ concentrations. Daycent simulations gave similar results | Fenn et al. 2008, 2010 |
| Mediterranean California | Mixed conifer forests (San Bernardino Mountains) | 17 | # | Reduced fine root biomass | Based on regression of throughfall N deposition and fine root biomass in ponderosa pine (also affected by co-occurring ozone) | Fenn et al. 2008; Grulke et al., 1998 |

continued

Table 19.6—continued

| Ecoregion | Ecosystem (Site) | CL for N $kg\ ha^{-1}\ yr^{-1}$ | Reliability | Response | Comments | Study |
|--|--|------------------------------------|-------------|--|---|--|
| Mediterranean California | Mixed conifer forests (San Bernardino Mountains) | 25.9 | # | Soil acidification; $pH \leq 4.6$ | Based on regression of throughfall N deposition and mineral soil H^+ | Breiner et al. 2007 |
| Mediterranean California | Mixed conifer forests (San Bernardino mountains) | 39 | (#) | Forest sustainability | Based on shifts in plant phenology and C allocation. Caused by combined effects of ozone and N deposition. Leads to increased bark beetle mortality and wildfire risk | Gruške and Baldurman 1999; Gruške et al. 1998, 2009; Jones et al. 2004 |
| Tropical and Subtropical Humid Forests | N-poor tropical and subtropical forests | 5-10 | (#) | Changes in community composition; NO_3^- leaching, N trace gas emissions | Critical load for N-poor forests based on estimates for Southeastern Coastal Plain forests | No direct studies ^a |
| Tropical and Subtropical Humid Forests | N-rich tropical and subtropical forests | <5-10 | (#) | NO_3^- leaching, N trace gas emissions | Critical load for N-rich forests should be lower than for N-poor forests based on possibility of N losses | No direct studies ^a |

^a The critical load is based on expert judgment and knowledge of ecosystems which may function similarly.

types that occur in most ecoregions in North America. In freshwater lakes and streams, phytoplankton, or algae that live in the water column, are sensitive to the chemical environment in which they reside. Many species can be used as indicators of the levels of nutrients or acidity because of individual species' preference for specific chemical conditions. Diatoms, unicellular plants that form the base of freshwater food webs, 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 percent are freshwater wetlands and 5 percent are estuarine or marine wetlands (FWS 2005). The species composition tends to differ 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.

Response to N inputs. 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 nitrogen:phosphorus (N:P) ratios, which can increase productivity of some species at the expense of others (Elser et al. 2009). As with the terrestrial ecosystems described above, freshwater nutrient responses are most evident where land use change and acidic deposition have been limited, thus most evidence of exceedance of N critical loads comes from the western United States (Chapter 18). As with terrestrial plants, some diatoms respond rapidly to an increase in available N. An example is dominance of two diatoms (*Asterionella formosa* and *Fragilaria crotonensis*) in numerous Rocky Mountain lakes with higher N, in contrast with 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 Tresseder 2008, US 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 (US 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 its 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 intertidal wetlands, such as salt marshes, and eelgrass (*Zostera* sp.) beds (Chapter 17).

Critical loads of N for freshwater ecosystems. 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 is 2 to 9 kg N ha⁻¹ yr⁻¹ (Chapter 18); the range reported for terrestrial and wetland ecosystems is much broader (Table 19.1). Critical loads for NO₃⁻ leaching from terrestrial ecosystems ranged from 4 to 17 kg N ha⁻¹ yr⁻¹ (Figure 19.9), but many sensitive freshwaters at high altitudes are found above the tree line where watershed N retention is limited due to little vegetation, poorly developed soils, short hydraulic residence time, and steep topography. Many hydrological factors including hydraulic residence time, N pool size, and conditions of water saturation affect N loss. 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

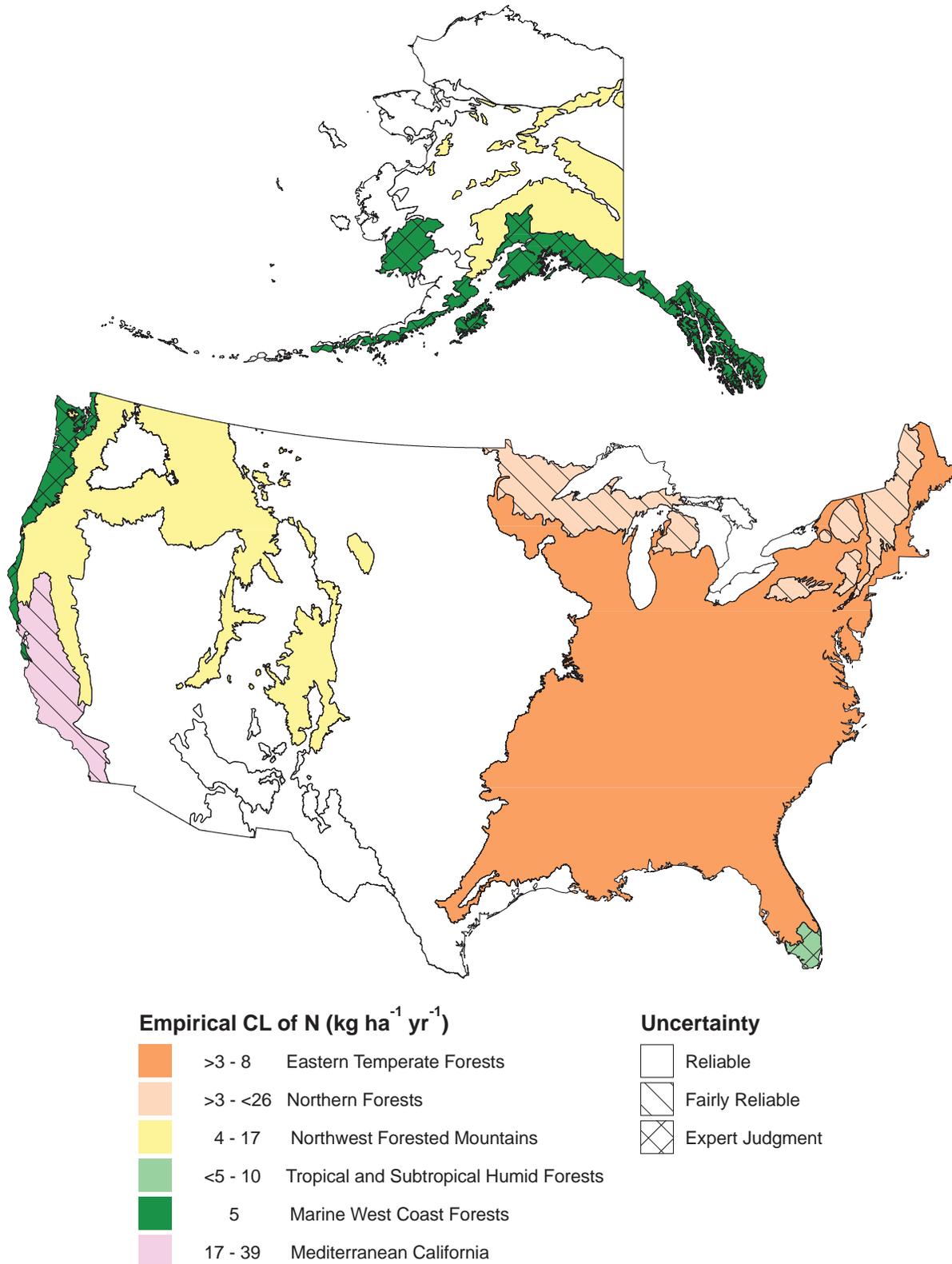


Figure 19.7—Map of critical loads (CL) for forest ecosystems by ecoregion in the United States. The range of critical loads reported for forest ecosystems is shown for each ecoregion; this map does not include the responses of mycorrhizal fungi, lichens, or understory herbaceous plants already represented. 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 color 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 color decreases. White areas lack data for critical loads determination for forest ecosystems.

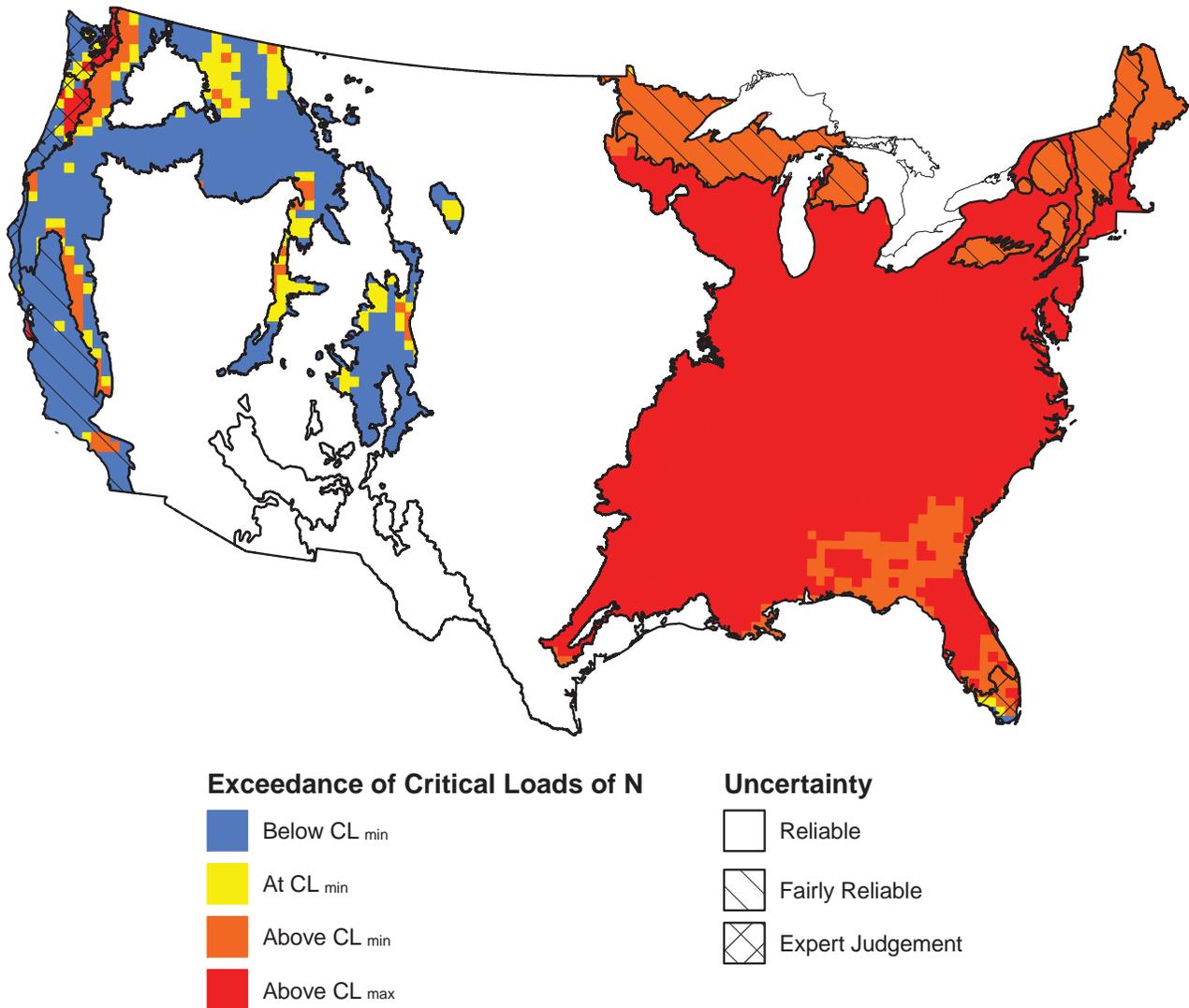


Figure 19.8—Map of exceedance of critical loads (CL) for forest ecosystems by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for forest ecosystems.

compared to soil N pools and are at least seasonally well mixed. They would, thus, be expected to have lower critical loads. Turnover times for N in mineral soil pools can be very long, and, as a result, buffer changes in soil solution that would affect terrestrial plants. Thus responses by terrestrial plants would not be expected to be as rapid as those of freshwater organisms.

Generally the most sensitive type of wetland to N deposition are freshwater wetlands, with critical loads that range from 2.7 to 14 kg N ha⁻¹ yr⁻¹ (Chapter

17). The nonvascular plant genus, *Sphagnum*, and the carnivorous pitcher plant (*Sarracenia* sp.) are the two species most commonly studied. The critical loads reported for freshwater wetlands (Chapter 17) fall between those reported for inland surface waters (Chapter 18) and those reported for terrestrial ecosystems. The critical load tends to be higher for 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

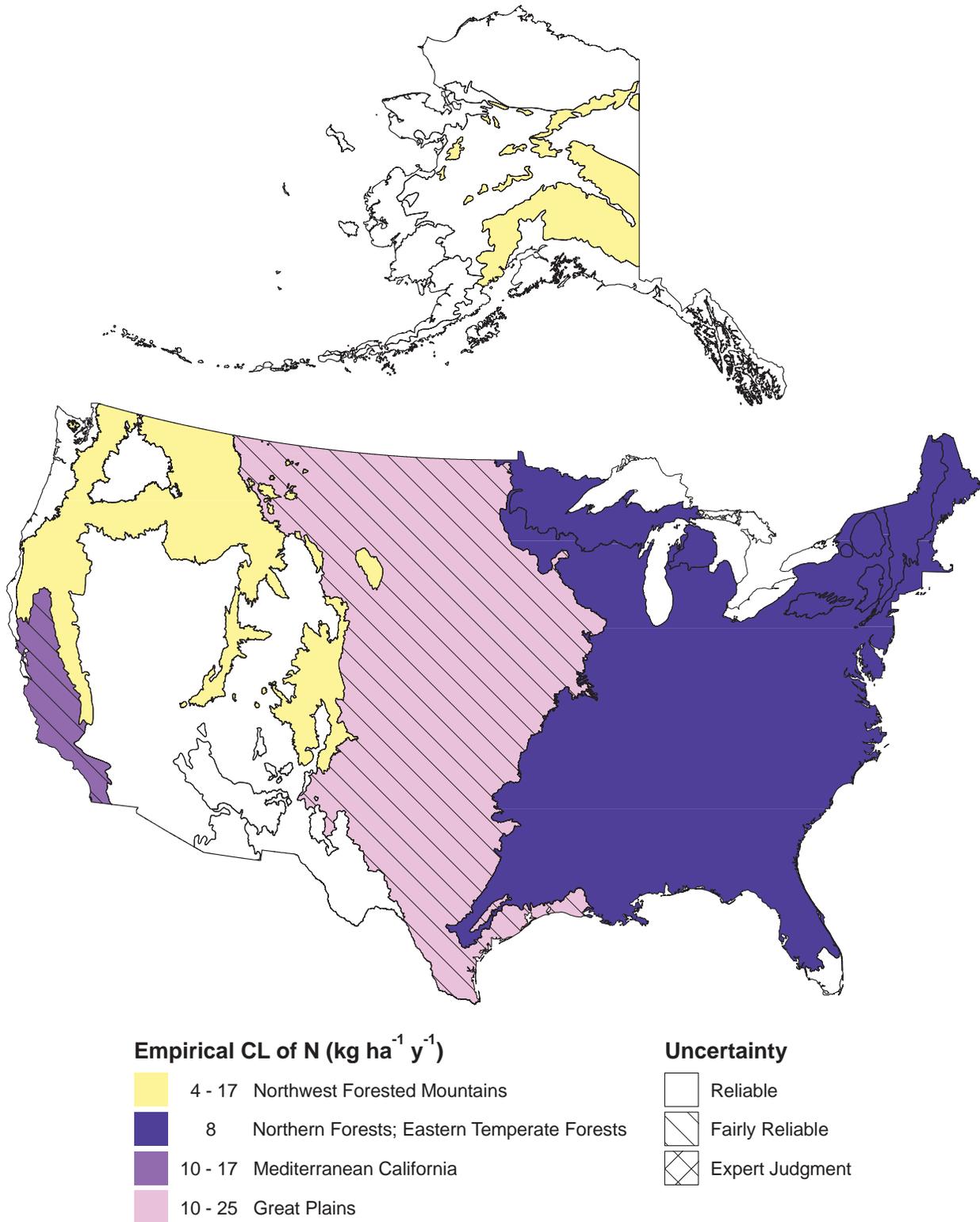


Figure 19.9—Map of critical loads (CL) for NO_3 -leaching by ecoregion in the United States. The range of critical loads based on increased nitrate leaching for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain “reliable” category, single hatching for the “fairly reliable” category, and double hatching for the “expert judgment” category. The color 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 color decreases. White areas lack data for critical loads determination for nitrate leaching.

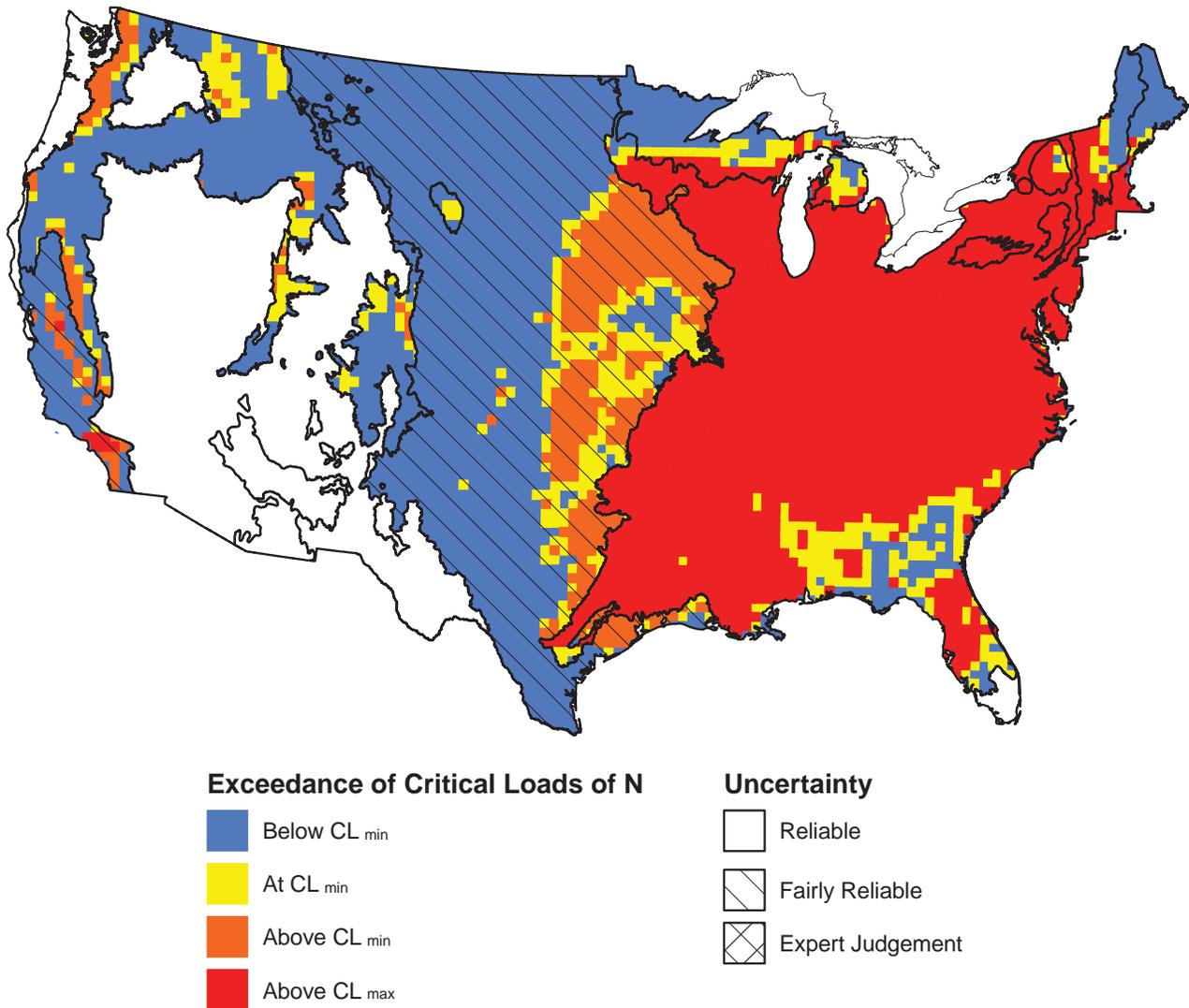


Figure 19.10—Map of exceedance of critical loads (CL) for NO_3^- leaching by ecoregion in the continental United States. Exceedance was calculated by subtracting critical loads from CMAQ nitrogen deposition. Exceedance (critical load - deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within ± 1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska. White areas lack data for critical loads determination for nitrate leaching.

N loading to plant growth and species composition on salt marsh and eelgrass habitat, the critical load ranges between 50 and 400 kg N ha⁻¹ yr⁻¹.

19.9 Comparison to Critical Loads in Europe

The critical loads for N deposition we report are consistently lower than those reported for Europe, with a few exceptions (Table 19.7). It is difficult to make the comparison between the United States and Europe because the ecosystem classification systems used are

not parallel. Empirical N critical loads for Europe (Bobbink et al. 2003) were reported at different scales using the European University Information Systems (EUNIS) than the U.S. critical loads: coarser for forests, for example, and finer for nonforests. Furthermore, the response variables and thresholds values of those variables are not always the same.

There are several reasons that N critical loads in Europe may be higher than in the United States. First, as discussed earlier, because N deposition in Europe has

Table 19.7—Comparison of critical loads for Europe and the United States. Reliability rating: ## reliable; # fairly reliable; # expert. Judgment. European data from Bobbink et al. 2003.

| North American ecoregion | Ecosystem component | Response | Critical Load <i>kg N ha⁻¹ yr⁻¹</i> | Reliability | European EUNIS code ^a | European ecosystem type or component | European indication of exceedance | European critical load <i>kg N ha⁻¹ yr⁻¹</i> | Reliability |
|---------------------------------|---|--|--|-------------|----------------------------------|---|--|---|-------------|
| Tundra | Prostrate dwarf shrub | Changes in CO ₂ exchange, cover, foliar N, and community composition of vascular plants | 1-3 | ## | F1 | Tundra | Changes in biomass, physiological effects, changes in species composition in moss layer, and decrease in lichens | 5-10 | # |
| Tundra | Lichens | Changes in lichen pigment production and ultrastructure, changes in lichen and bryophyte cover | 1-3 | (#) | F1 | Tundra | Changes in biomass, physiological effects, changes in species composition in moss layer, and decrease in lichens | 5-10 | # |
| Taiga | Lichens, algae, and bryophytes | Changes community composition, abundance, physiology, or ultrastructure. | 1-3 | # | G | Temperate and boreal forests: lichens and algae | Increase of algae, decrease of lichens | 10-15 | (#) |
| Taiga | Mycorrhizal fungi | Ectomycorrhizal fungal change in community structure | 5-7 | (#) | G | Temperate and boreal forests: mycorrhiza | Reduced sporocarp production, changed/reduced belowground species composition | 10-20 | (#) |
| Taiga | Shrublands | Change in shrub and grass cover, increased parasitism of shrubs | 6 | ## | F2 | Arctic, alpine and subalpine scrub habitats | Decline in lichens, mosses, and evergreen shrubs | 5-15 | (#) |
| Northern Forests | Lichens | Change in lichen community composition | 4-6 | (#) | G | Temperate and boreal forests: lichens and algae | Increase of algae, decrease of lichens | 10-15 | (#) |
| Northern Forests | Mycorrhizal fungi | Ectomycorrhizal fungal change in community structure | 5-7 | # | G | Temperate and boreal forests: mycorrhiza | Reduced sporocarp production, changed/reduced belowground species composition | 10-20 | (#) |
| Northern Forests | Herbaceous species | Loss of prominent species | >7 and <21 | # | G | Temperate and boreal forests: ground vegetation | Changed species composition, increase of nitrophilous species, increased susceptibility to parasites | 10-15 | # |
| Northern Forests | Coniferous forests | Increased surface water NO ₃ - leaching | 8 | ## | G | Coniferous forests | Increased NO ₃ ⁻ leaching | 10-15 | ## |
| Northern Forests | Hardwood forests | Increased surface water NO ₃ - leaching | 8 | ## | G | Deciduous forests | Increased NO ₃ ⁻ leaching | 10-15 | (#) |
| Northwestern Forested Mountains | Coniferous forests, Alaska: lichens | Lichen community change | 1.2-3.7 | (#) | G | Temperate and boreal forests: lichens and algae | Increase of algae, decrease of lichens | 10-15 | (#) |
| Northwestern Forested Mountains | Coniferous forests, non-Alaska: lichens | Lichen community change | 2.5-7.1 | ## | G | Temperate and boreal forests: lichens and algae | Increase of algae, decrease of lichens | 10-15 | (#) |
| Northwestern Forested Mountains | Subalpine forest | Increase in organic horizon N; higher potential net N mineralization rates | 4 | ## | G | Deciduous and coniferous forests | Increased N mineralization and nitrification | 10-15 | # |

| | | | | | | | | | |
|---------------------------------|---|--|-----------------|-----|-----------------|---|---|-------|-----|
| Northwestern Forested Mountains | Alpine vegetation: dry meadow tundra | Change in species composition | 4-10 | ## | E4.3 | Alpine or subalpine grasslands | Increase in tall graminoids, biodiversity change | 10-15 | (#) |
| Northwestern Forested Mountains | Mycorrhizal fungi | Ectomycorrhizal fungal change in community structure | 5-10 | (#) | G | Temperate and boreal forests: mycorrhiza | Reduced sporocarp production, changed/reduced belowground species composition | 10-20 | (#) |
| Marine West Coast Forests | Lichens | Epiphytic lichen community change | 2.7-9.2 | ## | G | Temperate and boreal forests: lichens and algae | Increase of algae, decrease of lichens | 10-15 | (#) |
| Eastern Forests | Lichens | Epiphytic lichen community change | 4-8 | (#) | G | Temperate and boreal forests: lichens and algae | Increase of algae, decrease of lichens | 10-15 | (#) |
| Eastern Forests | Southeastern Coastal Plain: mycorrhizal fungi | Ectomycorrhizal fungal community response | 5-10 | (#) | G | Temperate and boreal forests: mycorrhiza | Reduced sporocarp production, changed/reduced belowground species composition | 10-20 | (#) |
| Eastern Forests | Eastern hardwood forests | Increased surface water loading of NO ₃ | 8 | ## | G | Deciduous forests | Increased NO ₃ leaching | 10-15 | (#) |
| Eastern Forests | Eastern hardwood forest | Increased foliar percent N | >9 ^b | | G | Deciduous and coniferous forests | Changed N/macro nutrient ratios, decreased P, K, Mg; increased N concentration in foliar tissue | 15-20 | # |
| Eastern Forests | Herbaceous species | Herb layer changes | <17.5 | (#) | G | Temperate and boreal forests: ground vegetation | Changed species composition, increase of nitrophilous species, increased susceptibility to parasites | 10-15 | # |
| Great Plains | Tallgrass prairie | Biogeochemical N cycling, plant and insect community shifts | 5-15 | # | E1.7 | Non-Mediterranean dry acid and neutral closed grassland | Increase in graminoids, decline typical species | 10-20 | # |
| Great Plains | Mixed-grass prairie | Soil NO ₃ pools, leaching, plant community shifts | 10-25 | # | E1.26 | Sub-Atlantic semi-dry calcareous grassland | Increased tall grasses, decline in diversity; increased mineralisation and N leaching | 15-25 | ## |
| Wetlands | Bogs, fens, and swamps | Alterations in sphagnum accumulation and net primary productivity; alteration in pitcher plant community | 2.7-14 | # | D1 | Raised and blanket bogs | Increase vascular plants, decrease bryophytes, altered growth and species composition of mosses, increased N in peat and peat water | 5-10 | ## |
| Wetlands | Intertidal salt marsh | Salt marsh community structure, microbial activity and biogeochemistry | 63-400 | (#) | A2.64 and A2.65 | Pioneer and low-mid salt marshes | Increase late-successional species, increase productivity | 30-40 | (#) |
| Aquatic | Western high elevation lakes | Eutrophication | 2 | ## | C1.1 | Soft-water lakes | Isoetid species negatively affected | 5-10 | ## |
| Aquatic | Eastern high elevation lakes | Eutrophication | 8 | # | C1.1 | Soft-water lakes | Isoetid species negatively affected | 5-10 | ## |

^a EUNIS categories: A—Marine habitats; C—Inland surface water habitats; D—Mire, bog, and fen habitats; E—Grasslands and tall forb habitats; F—Heathland, scrub, and tundra habitats; G—Forest habitats
^b This value, from Boggs et al. (2005) is discussed in Chapter 10 as a response to N deposition. We did not include this value as a critical load in other tables, as the response threshold for detrimental ecological effects was not clear.

been considerably higher than that in the United States over many decades, it is difficult to find background or unimpacted sites as a basis of comparison. This means that, in some cases, the observed change in species composition does not reflect the initial response of a community to increased N inputs, but rather the response of a previously impacted community to further increases in N deposition. In addition, NH_4^+ inputs tend to be higher and represent a greater proportion of total N inputs in Europe. Note also that when dry deposition is underestimated in the United States, the N critical loads will also be underestimated, which would contribute to them being lower than those in Europe. Finally, since a greater proportion of the landscape in Europe, especially forested land, is managed, this may contribute to European N critical loads being higher, as N removal in harvesting results in greater N demand and storage during re-establishment of the forest stand.

Another possible explanation is that the response thresholds utilized in Europe are sometimes higher. A key example is lichen community responses: when a shift in community composition is considered the threshold of change, the N critical loads will be low. Some earlier work in Europe, in contrast, used a different biological threshold—the near extirpation of lichen species—leading to a higher N critical load (Bobbink et al. 2003). Another example of higher response thresholds used for setting critical loads in Europe relates to responses at the forest ecosystem level. Using a more sensitive endpoint, such as changes in N biogeochemistry interpreted as incipient responses of N saturation, led to a critical load $<4 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ in the Colorado Front Range (Rueth et al. 2003). This input is a subtle initial N enrichment response when compared to the magnitude of change for the critical loads thresholds in Europe (10 to $15 \text{ kg ha}^{-1} \text{ yr}^{-1}$).

19.10 Selecting Critical Loads for Natural Resource Decisions

Empirical critical loads may be determined for multiple receptors, responses, and response thresholds within an ecosystem. Thus, several critical loads may be determined for a given ecosystem type (various ecosystem components) when data are available. The

determination of these critical loads should be based on the best available scientific information. In section 19.7, we presented some of the factors that affect where the N critical load will fall within the reported range, which could be used to refine the critical load estimate for a given ecosystem. Several other issues need to be addressed in order to select empirical critical loads based on the values reported in this document. The objectives of different policy makers and resource managers will drive the decisions in selecting the N critical load most appropriate for a given area. First, the receptor of concern needs to be defined. The receptor may be a keystone species, the dominant species, the most sensitive species, or a threatened or endangered species. Next the response and response threshold must be set. In some cases, the response itself may be a significant change in the ecosystem (e.g., change in species composition) and in some cases, it may be an earlier stage response (e.g., increase in foliar N concentration). One challenge in determining the critical threshold for the response is that it can be difficult to define a pristine or unimpacted condition when much, or all, of the ecosystem has already experienced elevated N deposition. At this point, the policy makers or resource managers may also consider the degree of harm caused by a particular response; the determination of what level of harm is considered unacceptable is ultimately a policy decision.

Policy and resource management goals will determine the geographic extent and level of response that are considered unacceptable. In a conservation (e.g., wilderness) area, for example, any alteration in N cycling may be considered unacceptable—in these cases, when a range of N critical load values for a suite of resources and responses is presented, the lowest value is usually selected. Federal land managers responsible for Class I areas are required to “err of the side of protecting” these areas in determining the level of pollution these lands can tolerate. Other resource managers may choose to protect certain keystone species, threatened or endangered species, or species of economic or cultural significance. Finally, in some cases, the level of certainty about the critical load may determine which critical load is used.

Another approach for presenting maps of critical loads, which is used in Europe, is to map the critical load that would protect 95 percent of the habitat or ecosystem area (Hettelingh et al. 2008).

19.11 Use of Critical loads in the United States

In the United States, the critical loads approach has not been widely used as an approach for ecosystem protection. For example, the Clean Air Act does not specifically require development and use of critical loads in implementing and assessing environmental and natural resource management programs. Nevertheless, the critical loads approach is being explored at Federal, state, and international levels as an ecosystem assessment tool with great potential to simplify complex scientific information and effectively communicate with the policy community and the public. The critical loads approach can provide a useful lens through which to assess the results of current policies and programs and to evaluate the potential ecosystem-protection value of proposed policy options.

Recent developments in the United States indicate that critical loads might be emerging as a useful ecosystem protection and program assessment tool. In 2004, the National Research Council recommended that critical loads be examined as a tool for ecosystem protection (NRC 2004). Between 2002 and 2006, several Federal agencies convened conferences and workshops to review the experience with critical loads in other countries, discuss science and modeling efforts related to critical loads, and explore the possible future role of a critical loads approach as an air pollution control policy tool in the United States. A growing number of scientists are conducting research related to critical loads and are using various approaches to estimate critical loads in the United States.

Federal and state agencies are now exploring critical loads approaches to protect and manage sensitive ecosystems on Federal lands (Burns et al. 2008, Porter et al. 2005). In 2005, the U.S. Environmental Protection Agency (EPA) included a provision in its Nitrogen Dioxide Increment Rule enabling states to

propose the use of critical loads information as part of their air quality management approach, to satisfy requirements under Clean Air Act provisions regarding “prevention of significant deterioration.” The National Park Service is working with the Colorado Department of Public Health and Environment and EPA to address harmful impacts to air quality and other natural resources occurring in Rocky Mountain National Park in Colorado, and to reverse a trend of increasing N deposition. The National Park Service has established a resource management goal, linked to a critical load for wet N deposition of $1.5 \text{ kg ha}^{-1} \text{ yr}^{-1}$ for high elevation aquatic ecosystems. Resource managers within the U.S. Forest Service use critical loads to serve as a practical guideline when considering the potential impacts from new sources of emissions on resources in Class I areas. Forest Service resource managers are also using critical loads in the national watershed condition assessment process to identify potential areas on national forests for mitigation of ecosystem impairment. Several states have developed Total Maximum Daily Load (TMDL) estimates for acidic deposition to alleviate surface waters that are impaired due to elevated acidity (i.e., low pH, low ANC).

The critical loads approach recently has been utilized for ecosystem assessments within the broader environmental policy context as well. In 2005, for example, the Clean Air Act Advisory Committee recommended that the EPA use critical loads as a means to evaluate progress in reducing ecological impacts of air pollution. As a result, EPA’s 2007 and 2008 Annual Acid Rain Program progress reports utilized critical loads as a means of assessing the extent to which implementation of Title IV of the 1990 Clean Air Act Amendments has decreased S and N sufficiently to protect acid-sensitive ecosystems in the Adirondack Mountain and Central Appalachian regions. The critical loads approach also has entered the realm of bilateral environmental policy. In 2008, the ninth biennial progress report completed under the 1991 United States-Canada Air Quality Agreement included estimates of critical loads in acid-sensitive lakes in the northeastern United States. While the Canadian government routinely reports critical load data, this was the first time critical load data for the United States were

reported in a progress report prepared by the bilateral U.S.-Canada Air Quality Committee (Environment Canada 2008).

19.12 Summary

In an analysis of the nine major environmental challenges facing humanity, only three have clearly exceeded safe operating boundaries: biodiversity loss, increased N, and climate change (Rockström et al. 2009). Because most terrestrial and many aquatic ecosystems are N limited under unpolluted conditions, increases in N input to ecosystems are likely to have an impact. Increased N deposition can cause a shift in the processing and movement of N (function) and to the physical composition (structure) of the ecosystem as evidenced by the examples below.

Large parts of the eastern United States, as well as localized areas in the West, are experiencing N deposition that exceeds the critical load for sensitive ecosystem components. The resources most threatened by elevated N deposition include freshwater diatoms, lichens, bryophytes, and herbaceous plants. 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 favor 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 most current studies.

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 butterfly population (Fenn et al. 2010, Weiss 1999). In Joshua Tree National Park and adjacent deserts in

southern California, elevated N deposition favors 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 in this fragile community (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 eutrophication of freshwater ecosystems (Saros et al. 2010; 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 California, where elevated N deposition and arid low-biomass ecosystems coincide (e.g., coastal sage scrub, grassland, desert), N-enhanced growth of invasive species resulting in major alterations of plant communities, conversion of vegetation type, and 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 that N deposition contributes to multiple stress complexes and has decreased forest sustainability in California (Grulke et al. 2009) and in North Carolina (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). Another example of N deposition interactions with other forest stressors is the observation that increased NO_3^- leaching and nitrification contribute to soil acidification and depletion of available nutrient cations which have negative effects on tree growth, vigor, and cold tolerance in some forests. Elevated NO_3^- concentrations in surface water and groundwater may diminish drinking water quality, although the drinking water standard is often only exceeded for brief periods, for example when N saturated watersheds are disturbed (e.g., fire or harvesting). 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 consequences of climate change.

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 nitric oxide (NO), an ozone (O₃) precursor; nitrous oxide (N₂O), a long-lived greenhouse gas; as well as declines in soil uptake of methane (CH₄), another long-lived greenhouse gas (Liu and Greaver 2009).

The above examples provide compelling evidence for significant alteration of ecosystem structure and function in ecoregions across the United States due to elevated N deposition. To protect ecosystems from harm caused by N deposition, it is necessary to identify the level of N deposition which would lead to detrimental ecological effects. Empirical critical loads for N provide a valuable approach for evaluating the risk of harm to ecosystems. This approach has been used broadly in Europe (Bobbink et al. 2003, UBA 2004) and has the advantage of being scientifically based on observed responses. This link to actual ecosystem responses is especially beneficial in resource management and policy contexts.

This report provides the first comprehensive assessment of empirical critical loads of N for ecoregions across the United States. It represents an important step toward providing policy makers and resource managers with a tool for ecosystem protection as suggested by the National Research Council (NRC 2004).

19.13 Future Research Priorities

The principal knowledge gaps that limit our understanding of N impacts on ecosystems include poor quantification of total N deposition (especially in deposition hotspots) and the paucity of long-term, low N-fertilization studies and adequate deposition gradient studies. A higher density of long-term, low N fertilization studies, as well as long-term and larger scale gradient studies across both a greater diversity of

ecosystem types and regions of low N deposition, are necessary to develop dose response curves that would better define critical loads and the associated uncertainty. In the United States, observations of ecosystem response to N inputs are particularly limited in the Tundra, Taiga, and North American Desert ecoregions.

Other important issues include:

- The differential response to reduced (NH_x) versus oxidized (NO_y) N inputs. Because some plants are particularly sensitive to NH_x inputs (Krupa 2003) while others are more sensitive to NO_y (Nordin et al. 2006), assembling more comprehensive data about these species-specific responses would allow more accurate assessment of potential risks to ecosystems in relation to the major N emissions sources. Oxidized and reduced N forms also result in different levels of acidification.
- Impacts on plant biodiversity in forests have not been well described, in part because of the difficulty of assessing such changes in ecosystems with longer-lived organisms, and in part, because in many of these ecosystems the herbaceous plants have already been altered by historical N deposition, other pollutants, or habitat alteration.
- Effects of N deposition on forest growth and sustainability. Insufficient data are available to determine critical loads for the effects of increasing N fertility on pest outbreaks, drought, cold tolerance, tree vigor, and multiple stress complexes in general.
- Identification of mechanisms that control plant and ecosystem responses to N deposition. This is a necessary step in refining critical loads estimates, improving their reliability, and laying the groundwork for more complex dynamic models, which are necessary for broad scale assessments, including detailed national maps of empirical critical loads for N.

The objective of future critical-loads-driven research should be to fill in gaps in data and improve the

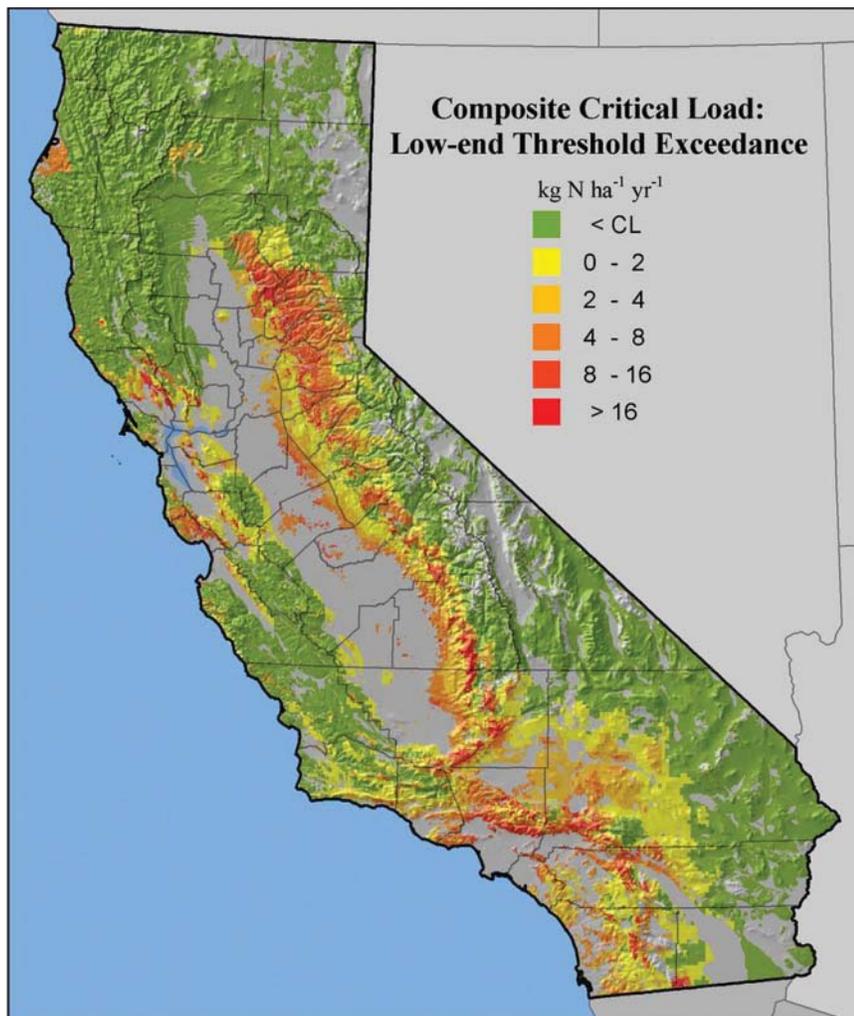


Figure 19.11—Composite showing critical load exceedance for seven vegetation types in California (Fenn et al. 2010).

reliability of estimates. When more data are available, especially data of higher reliability, it will be possible to make a map of empirical critical loads of N such as that developed for California (Figure 19.11; Fenn et al. 2010). This map also utilized N deposition modeled at a much finer grid (4 km x 4 km). One approach for assembling the data necessary to estimate critical loads is using systematically sampled large scale studies (for example the U.S. Forest Service FIA grid sampling) to ensure that a broad gradient in N deposition, climate, and other variables are included in the dataset generated (e.g., Geiser and Neitlich 2007, Jovan 2008). This approach would allow extrapolation of the N critical loads to a broad area with confidence. Better understanding of when the “baseline” response has been altered by prior N deposition is necessary to identify empirical critical loads using N deposition gradient or N addition studies. Long-term monitoring is also necessary

to evaluate the scope of particular responses and to assess future responses to reductions in N deposition. The accuracy of empirical N critical loads is limited by the accuracy of the N deposition values used. Thus, improving estimates of total N deposition is essential for improving empirical critical loads and exceedance estimates.

Thus, the highest research priorities should be:

- (1) Lichens: systematic sampling of lichens in areas where there are few data in combination with analyzing existing FIA data could yield very useful results for this sensitive indicator.
- (2) Diatoms in lake sediments and phytoplankton in lakes: diatoms preserved in lake sediments can be used to identify when and at what atmospheric N deposition amounts critical

thresholds were crossed in the past. The approach has applications far beyond the few locations where it has been applied. Phytoplankton in lakes respond rapidly to changes in limiting nutrients, and far more studies are needed to show how (and how much) N deposition is needed to affect the N:P stoichiometric ratio and subsequent shifts in food webs and ecological processes in oligotrophic lakes. Equally important are studies of whether the removal of N deposition allows the return of N-limited conditions and oligotrophic phytoplankton. A final and key research priority for lakes are experiments to determine the effects of atmospheric N deposition on algal biodiversity.

- (3) Herbaceous species: research is needed to identify the most responsive species across a variety of ecosystem types.
- (4) Identifying indicator species in general: species which allow evaluation of the ecosystem condition are especially useful for empirical N critical loads estimates.
- (5) Long-term low N addition experiments: more long-term low N fertilization studies will help make more accurate determinations of critical loads.

LITERATURE CITED

- Aber, J.; McDowell, W.; Nadelhoffer, K.; Magill, A.; Berntson, G.; Kamakea, M.; McNulty, S.; Currie, W.; Rustad, L.; Fernandez, I. 1998. **Nitrogen saturation in temperate forest ecosystems.** *BioScience*. 48: 921-934.
- Aber, J.D.; Goodale, C.L.; Ollinger, S.V.; Smith, M.-L.; Magill, A.H.; Martin, M.E.; Hallet, R.A.; Stoddard, J.L. 2003. **Is nitrogen deposition altering the nitrogen status of Northeastern forests?** *BioScience*. 53(4): 375-389.
- Aber, J.D.; Nadelhoffer, K.J.; Steudler, P.; Melillo, J.M. 1989. **Nitrogen saturation in northern forest ecosystems.** *BioScience*. 39: 378-386.
- Adams, M.B.; DeWalle, D.R.; Peterjohn, W.T.; Gilliam, F.S.; Sharpe, W.E.; Williard, K.W.J. 2006. **Soil chemical responses to experimental acidification treatments.** In: Adams, M.B.; DeWalle, D.R.; Hom, J.L., eds. *The Fernow watershed acidification study*. Dordrecht, The Netherlands: Springer: 41-69.
- Aldous, A.R. 2002. **Nitrogen retention by *Sphagnum* mosses: responses to atmospheric nitrogen deposition and drought.** *Canadian Journal of Botany*. 80: 721-731.
- Allen, E.B.; Rao, L.E.; Steers, R.J.; Bytnerowicz, A.; Fenn, M.E. 2009. **Impacts of atmospheric nitrogen deposition on vegetation and soils in Joshua Tree National Park.** In: Webb, R.H.; Fenstermaker, L.F.; Heaton, J.S.; Hughson, D.L.; McDonald, E.V.; Miller, D.M., eds. *The Mojave Desert: Ecosystem processes and sustainability*. Las Vegas: University of Nevada Press: 78-100.
- Allen, E.B.; Temple, P.J.; Bytnerowicz, A.; Arbaugh, M.J.; Sirulnik, A.G.; Rao, L.E. 2007. **Patterns of understory diversity in mixed coniferous forests of southern California impacted by air pollution.** *The Scientific World Journal*. 7(S1): 247-263.
- Amaranthus, M.P. 1998. **The importance and conservation of ectomycorrhizal fungal diversity in forest ecosystems: Lessons from Europe and the Pacific Northwest.** Gen. Tech. Rep. PNW-431. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 15 p.
- Arens, S.J.T.; Sullivan, P.F.; Welker, J.M. 2008. **Nonlinear responses to nitrogen and strong interactions with nitrogen and phosphorus additions drastically alter the structure and function of a high arctic ecosystem.** *Journal of Geophysical Research-Biogeosciences* 113: G03509.
- Baker, J.P.; Van Sickle, J.; Gagen, C.J.; Baldigo, B.P.; Bath, D.W.; Carline, R.F.; DeWalle, D.R.; Kretser,

- W.A.; Murdoch, P.S.; Sharpe, W.E.; Simonin, H.A.; Wigington, P.J. 1996. **Episodic acidification of small streams in the northeastern United States: Effects on fish populations.** *Ecological Applications*. 6: 422-437.
- Baron, J.S. 2006. **Hindcasting nitrogen deposition to determine ecological critical load.** *Ecological Applications*. 16(2): 433-439.
- Baron, J.S.; Ojima, D.S.; Holland, E.A.; Parton, W.J. 1994. **Analysis of nitrogen saturation potential in Rocky Mountain tundra and forest: Implications for aquatic systems.** *Biogeochemistry*. 27: 61-82.
- Baron, J.S.; Rueth, H.M.; Wolfe, A.M.; Nydick, K.R.; Allstott, E.J.; Minear, J.T.; Moraska, B. 2000. **Ecosystem responses to nitrogen deposition in the Colorado Front Range.** *Ecosystems*. 3: 352-368.
- Barret, J.E.; Burke, I.C. 2002. **Nitrogen retention in semiarid ecosystems across a soil organic-matter gradient.** *Ecological Applications*. 12: 878-890.
- Belyazid S.; Westling, O.; Sverdrup, H. 2006. **Modelling changes in forest soil chemistry at 16 Swedish coniferous forest sites following deposition reduction.** *Environmental Pollution*. 144: 596-609.
- Berryman, S.; Straker, J. 2008. **Nitrogen loading and terrestrial vegetation—assessment of existing regional monitoring and recommendations.** Sidney, BC: Submitted by CE Jones and Associates.
- Berryman, S.; Geiser, L.; Brenner, G. 2004. **Depositional gradients of atmospheric pollutants in the Athabasca Oil Sands region, Alberta, Canada: an analysis of lichen tissue and lichen communities.** Lichen Indicator Pilot Program 2002-2003. Final report submitted to the Terrestrial Environmental Effects Monitoring (TEEM) Science sub-committee of the Wood Buffalo Environmental Association (WBEA). Fort McMurray, AB, Canada: Wood Buffalo Environmental Association.
- Blett, T.; Geiser, L.; Porter, E. 2003. **Air pollution-related lichen monitoring in national parks, forests, and refuges: guidelines for studies intended for regulatory and management purposes.** Tech. Rep. NPS-D2292. Denver, CO: U.S. Department of the Interior, National Park Service, Air Resources Division and U.S. Fish and Wildlife Service, Air Quality Branch; Corvallis, Oregon: U.S. Department of Agriculture, Forest Service. 26 p.
- Bobbink, R.; Ashmore, M.; Braun, S.; Flückinger, W.; van den Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbink, R., eds. *Empirical critical loads for nitrogen.* Environmental Documentation No. 164. Berne, Switzerland: Swiss Agency for the Environment, Forests, and Landscape: 43-170.
- Bobbink R.; Boxman D.; Fremstad E.; Heil G.; Houdijk A.; Roelofs J. 1992. **Critical loads for nitrogen eutrophication of terrestrial and wetland ecosystems based upon changes in vegetation and fauna.** In: Grennfelt, P.; Thörnelöf, E., eds. *Critical loads for nitrogen.* Copenhagen: Nordic Council of Ministers: 111-159.
- Bobbink, R.; Hicks, K.; Galloway, J.N.; Spranger, T.; Alkemade, R.; Ashmore, M.; Bustamante, M.M.C.; Cinderby, S.; Davidson, E.A.; Dentener, F.; Emmett, B.; Erisman, J.-W.; Fenn, M.; Gilliam, F.; Nordin, A.; Pardo, L.; de Vries, W. 2010. **Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis.** *Ecological Applications*. 20(1): 30-59.
- Bobbink, R.; Hornung, M.; Roelofs, J.G.M. 1998. **The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation.** *Journal of Ecology*. 86: 738.
- Boggs, J.L.; McNulty, S.G.; Gavazzi, M.J.; Moore, J. 2005. **Tree growth, foliar chemistry, and nitrogen cycling across a nitrogen deposition gradient in southern Appalachian deciduous forests.** *Canadian Journal of Forest Research*. 35: 1901-1913.

- Boonpragob, K.; Nash, T.H. III; Fox, C.A. 1989. **Seasonal deposition patterns of acidic ions and ammonium to the lichen *Ramalina menziesii* Tayl. in southern California.** *Environmental and Experimental Botany*. 29: 187-197.
- Bowman, W.D.; Larson, J.R.; Holland, K.; Wiedermann, M.; Nieves, J. 2006. **Nitrogen critical loads for alpine vegetations and ecosystem response- are we there yet?** *Ecological Applications*. 16(3): 1183-1193.
- Breiner, J.; Gimeno, B.S.; Fenn, M. 2007. **Calculation of theoretical and empirical nutrient N critical loads in the mixed-conifer ecosystems of southern California.** *The Scientific World Journal*. 7(S1): 198-205.
- Burns, D.A.; Blett, T.; Haeuber, R.; Pardo, L.H. 2008. **Critical loads as a policy tool for protecting ecosystems from the effects of air pollutants.** *Frontiers in Ecology and the Environment*. 6: 156-159.
- Byun, D.W.; Ching, J.K.S., eds. 1999. **Science algorithms of the EPA models-3 Community Multiscale Air Quality model (CMAQ) modeling system. EPA/600/R-99/030.** Washington, DC: U.S. Environmental Protection Agency, Office of Research and Development. Available at <http://www.epa.gov/asmdnerl/CMAQ/CMAQscienceDoc.html> (Accessed May 12, 2010).
- Byun, D.; Schere, K.L. 2006. **Review of the governing equations, computational algorithms, and other components of the Models-3 Community Multiscale Air Quality (CMAQ) modeling system.** *Applied Mechanics Reviews*. 59: 51-77.
- Caffrey, J.M.; Murrell, M.C.; Wigand, C.; McKinney, R. 2007. **Effect of nutrient loading on biogeochemical and microbial processes in a New England salt marsh.** *Biogeochemistry*. 82: 251-264.
- Cape, J.N.; van der Eerden, L.J.; Sheppard, L.J.; Leith, I.D.; Sutton, M.A. 2009. **Reassessment of critical levels for atmospheric ammonia.** In: Sutton M.; Reis, S.; Baker, S.M.H., eds. *Atmospheric ammonia*. Dordrecht, The Netherlands: Springer Science: 15-40.
- Clark, C.M.; Hobbie, S.; Venterea, R.; Tilman, D. 2009. **Long-lasting effects on N cycling 12 years after treatments cease despite minimal N retention.** *Global Change Biology*. 15: 1755-1766.
- Clark, C.M.; Tilman, D. 2008. **Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands.** *Nature*. 451: 712-715.
- Clark, J.E.; Hellgren, E.C.; Jorgensen, E.E.; Leslie, D.M. 2005. **Population dynamics of harvest mice (*Reithrodontomys fulvescens* and *R. montanus*) across a nitrogen-amended old field.** *American Midland Naturalist*. 154: 240-252.
- Clark, J.E.; Hellgren, E.C.; Jorgensen, E.E.; Tunnell, S.J.; Engle, D.M.; Leslie, D.M. 2003. **Population dynamics of hispid cotton rats (*Sigmodon hispidus*) across a nitrogen-amended landscape.** *Canadian Journal of Zoology-Revue Canadienne De Zoologie*. 81: 994-1003.
- CEC (Commission for Environmental Cooperation). 1997. **Ecological regions of North America. Toward a common perspective.** Montreal, QC, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).
- Cornelissen, J.H.C.; Lang, S.I.; Soudzilovskaia, N.A.; During, H.J. 2007. **Comparative cryptogam ecology: A review of bryophyte and lichen traits that drive biogeochemistry.** *Annals of Botany*. 99: 987-1001.
- de Vries, W.; Kros, J.; Reinds, G.J.; Wamelink, W.; van Dobben, H.; Bobbink, R.; Emmett, B.; Smart, S.; Evans, C.; Schlutow, A.; Kraft, P.; Belyazid, S.; Sverdrup, H.; Hinsberg, A. van; Posch, M.; Hettelingh, J.P. 2007. **Developments in deriving critical limits and modeling critical loads of**

- nitrogen for terrestrial ecosystems in Europe.** Alterra Report 1382 [Alterra-rapport 1382]. Wageningen, The Netherlands: Wageningen University, Alterra. 206 p.
- de Vries, W.; Wamelink, W.; van Dobben, H.; Kros, H.; Reinds, G.J.; Mol-Dijkstra, J.; Smart, S.; Evans, C.; Rowe, E.; Belyazid, S.; Sverdrup, H.; van Hinsberg, A.; Posch, M.; Hettelingh, J.-P.; Spranger, T.; Bobbink, R. 2010. **Use of dynamic soil-vegetation models to assess impacts of nitrogen deposition on plant species composition: an overview.** *Ecological Applications*. 20 (1): 60-79.
- Dighton, J.; Tuininga, A.R.; Gray, D.M.; Huskins, R.E.; Belton, T. 2004. **Impacts of atmospheric deposition on New Jersey pine barrens forest soils and communities of ectomycorrhizae.** *Forest Ecology and Management*. 201: 131-144.
- Driscoll, C.T.; Whitall, D.; Aber, J.; Boyer, E.; Castro, M.; Cronan, C.; Goodale, C.L.; Groffman, P.; Hopkinson, C.; Lambert, K.; Lawrence, G.; Ollinger, S. 2003. **Nitrogen pollution in the northeastern United States: sources, effects, and management options.** *BioScience*. 53: 357-374.
- Duan, L. 2009. **Empirical critical loads of nitrogen in China.** In: Proceedings from a workshop on nitrogen deposition, critical loads, and biodiversity; 2009 November 16-18; Edinburgh, Scotland. Available at http://www.rivm.nl/thema/images/Poster_lei_duan_icpmm_2010_tcm61-48704.pdf [Poster] (Accessed April 21, 2011).
- Dupont, J.; Clair, T.A.; Gagnon, C.; Jeffries, D.S.; Kahl, J.S.; Nelson, S.; Peckenham, J. 2005. **Estimation of critical loads of acidity for lakes in northeastern United States and eastern Canada.** *Environmental Monitoring Assessment*. 109: 275-292.
- Egerton-Warburton, L.M.; Allen, E.B. 2000. **Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient.** *Ecological Applications*. 10: 484-496.
- Egerton-Warburton, L.M.; Graham, R.C.; Allen, E.B.; Allen, M.F. 2001. **Reconstruction of the historical changes in mycorrhizal fungal communities under anthropogenic nitrogen deposition.** *Proceedings of the Royal Society of London*. B268: 2479-2484.
- Elser, J.J.; Anderson, T.; Baron, J.S.; Bergström, A.-K.; Kyle, M.; Nydick, K.R.; Steger, L.; Hessen, D.O. 2009. **Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition.** *Science*. 326: 835-837.
- Emmett, B.A.; Reynolds, B. 2003. **The role of models in addressing critical N loading to ecosystems.** In: Canham, C.D.; Cole, J.J.; Lauenroth, W.K., eds. *Models in ecosystem science*. Princeton, NJ: Princeton University Press: 308-326.
- Environment Canada. 2008. **Canada-United States air quality agreement progress report 2008.** Ottawa, ON, Canada, and Washington, DC: International Joint Commission. Available at http://www.ec.gc.ca/cleanair-airpur/caol/canus/report/2008CanUs_eng/tdm-toc_eng.cfm (Accessed June 6, 2009).
- Epstein, H.E.; Burke, I.C.; Mosier, A.R. 2001. **Plant effects on nitrogen retention in shortgrass steppe 2 years after ¹⁵N addition.** *Oecologia*. 128: 422-430.
- Falkengren-Grerup, U. 1995. **Interspecies differences in the preference of ammonium and nitrate in vascular plants.** *Oecologia*. 102: 305-311.
- Fenn, M.E.; Allen, E.B.; Weiss, S.B.; Jovan, S.; Geiser, L.; Tonnesen, G.S.; Johnson, R.F.; Rao, L.E.; Gimeno, B.S.; Yuan, F.; Meixner, T.; Bytnerowicz, A. 2010. **Nitrogen critical loads and management alternatives for N-impacted ecosystems in California.** *Journal of Environmental Management*. 91(12): 2404-2423.
- Fenn, M.E.; Baron, J.S.; Allen, E.B.; Rueth, H.M.; Nydick, K.R.; Geiser, L.; Bowman, W.D.; Sickman, J.O.; Meixner, T.; Johnson, D.W.; Neitlich, P. 2003a. **Ecological effects of nitrogen deposition in the western United States.** *BioScience*. 53(4): 404-420.

- Fenn, M.E.; de Bauer, L.I.; Quevedo-Nolasco, A.; Rodriguez-Frausto, C. 1999. **Nitrogen and sulfur deposition and forest nutrient status in the Valley of Mexico.** *Water, Air, and Soil Pollution*. 113: 155-174.
- Fenn, M.E.; de Bauer, L.I.; Zeller, K.; Quevedo, A.; Rodríguez, C. and Hernández-Tejeda, T. 2002. **Nitrogen and sulfur deposition in the Mexico City air basin: Impacts on forest nutrient status and nitrate levels in drainage waters.** In: Fenn, M.E.; de Bauer, L.I.; Hernández-Tejeda, T., eds. *Urban air pollution and forests: Resources at Risk in the Mexico City air basin.* Ecological Studies Series, Volume 156. New York, NY: Springer-Verlag: 298-319.
- Fenn, M.E.; Haueber, R.; Tonnensen, G.S.; Baron, J.S.; Grossman-Clarke, S.; Hope, D.; Jaffe, D.A.; Copeland, S.; Geiser, L.; Rueth, H.M.; Sickman, J.O. 2003b. **Nitrogen emission, deposition, and monitoring in the Western United States.** *Bioscience*. 53(4): 391-403.
- Fenn, M.E.; Jovan, S.; Yuan, F.; Geiser, L.; Meixner, T.; Gimeno, B.S. 2008. **Empirical and simulated critical loads for nitrogen deposition in California mixed conifer forests.** *Environmental Pollution*. 155: 492-511.
- Fenn, M.E.; Poth, M.A. 1999. **Temporal and spatial trends in streamwater nitrate concentrations in the San Bernardino Mountains, southern California.** *Journal of Environmental Quality*. 28: 822-836.
- Fenn, M.E.; Poth, M.A.; Bytnerowicz, A.; Sickman, J.O.; Takemoto, B.K. 2003c. **Effects of ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra Nevada.** In: Bytnerowicz, A.; Arbaugh, M.J.; Alonso, R., eds. *Developments in environmental science, volume 2: Ozone air pollution in the Sierra Nevada: Distribution and effects on forests.* Amsterdam: Elsevier: 111-155.
- FWS (U.S. Fish and Wildlife Service). 2005. **Status and trends of wetlands in the conterminous United States 1998 to 2004.** Washington, DC: U.S. Department of Interior, Fish and Wildlife Service. 112 p.
- Galloway, J.N. 1998. **The global nitrogen cycle: changes and consequences.** *Environmental Pollution*. 102: 15-24.
- Galloway, J.N.; Aber, J.D.; Erisman, J.W.; Seitzinger, S.P.; Howarth, R.W.; Cowling, E.B.; Cosby, B.J. 2003. **The nitrogen cascade.** *BioScience*. 53: 341-356.
- Geiser, L.H.; Ingersoll, A.R.; Bytnerowicz, A.; Copeland, S.A. 2008. **Evidence of enhanced atmospheric ammoniacal nitrogen in Hells Canyon NRA: Implications for natural and cultural resources.** *Journal of the Air & Waste Management Association*. 58: 1223-1234.
- Geiser, L.H.; Jovan, S.E.; Glavich, D.A.; Porter, M. 2010. **Lichen-/based critical loads for atmospheric nitrogen deposition in Western Oregon and Washington Forests, USA.** *Environmental Pollution*. 158: 2412-2421.
- Geiser, L.H.; Neitlich, P.N. 2007. **Air pollution and climate gradients in western Oregon and Washington indicated by epiphytic macrolichens.** *Environmental Pollution*. 145: 203-218.
- Gilliam, F.S. 2006. **Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition.** *Journal of Ecology*. 94: 1176-1191.
- Gilliam, F.S. 2007. **The ecological significance of the herbaceous layer in forest ecosystems.** *BioScience*. 57: 845-858.
- Gilliam, F.S.; Adams, M.B.; Yurish, B.M. 1996. **Ecosystem nutrient responses to chronic nitrogen inputs at Fernow Experimental Forest, West Virginia.** *Canadian Journal of Forest Research*. 26: 196-205.

- Gilliam, F.S.; Hockenberry, A.W.; Adams, M.B. 2006. **Effects of atmospheric nitrogen deposition on the herbaceous layer of a central Appalachian hardwood forest.** *Journal of the Torrey Botanical Society*. 133: 240-254.
- Glavich, D.A.; Geiser, L.H. 2008. **Potential approaches to developing lichen-based critical loads and levels for nitrogen, sulfur and metal-containing atmospheric pollutants in North America.** *The Bryologist*. 111: 638-649.
- Gotelli, N.J.; Ellison, A.M. 2002. **Nitrogen deposition and extinction risk in the northern pitcher plant, *Sarracenia purpurea*.** *Ecology*. 83: 2758-2765.
- Gotelli, N.J.; Ellison, A.M. 2006. **Forecasting extinction risk with nonstationary matrix models.** *Ecological Applications*. 16: 51-61.
- Grulke, N.E.; Andersen, C.P.; Fenn, M.E.; and Miller, P.R. 1998. **Ozone exposure and nitrogen deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains, California.** *Environmental Pollution*. 103: 63-73.
- Grulke, N.E.; Balduman, L. 1999. **Deciduous conifers: High N deposition and O₃ exposure effects on growth and biomass allocation in ponderosa pine.** *Water, Air and Soil Pollution*. 116: 235-248.
- Grulke, N.E.; Minnich, R.A.; Paine, T.D.; Seybold, S.J.; Chavez, D.J.; Fenn, M.E.; Riggan, P.J.; Dunn, A. 2009. **Air pollution increases forest susceptibility to wildfires: A case study in the San Bernardino Mountains in southern California.** In: Bytnerowicz, A.; Arbaugh, M.J.; Riebau, A.R.; Andersen, C., eds. *Wildland fires and air pollution. Developments in environmental science, Volume 8.* Amsterdam: Elsevier: 365-403.
- Hettelingh, J.-P.; Posch, M.; Slootweg, J., eds. 2008. **Critical load, dynamic modelling and impact assessment in Europe. CCE Status Report 2008.** Bilthoven, The Netherlands: Netherlands Environmental Agency, Coordination Centre for Effects. Netherlands Environmental Assessment Agency. 231 p. Available at www.rivm.nl/cce (Accessed March 30, 2011).
- Hurd, T.M.; Brach, A.R.; Raynal, D.J. 1998. **Response of understory vegetation of Adirondack forests to nitrogen additions.** *Canadian Journal of Forest Research*. 28: 799-807.
- Hyvärinen, M.; Walter, B.; Koopmann, R. 2003. **Impact of fertilisation on phenol content and growth rate of *Cladonia stellaris*: a test of the carbon-nutrient balance hypothesis.** *Oecologia*. 134: 176-181.
- Inouye, R.S. 2006. **Effects of shrub removal and nitrogen addition on soil moisture in sagebrush steppe.** *Journal of Arid Environments*. 65: 604-618.
- Jones, M.E.; Paine, T.D.; Fenn, M.E.; Poth, M.A. 2004. **Influence of ozone and nitrogen deposition on bark beetle activity under drought conditions.** *Forest Ecology and Management*. 200: 67-76.
- Jorgensen, E.E.; Holub, S.M.; Mayer, P.M.; Gonsoulin, M.E.; Silva, R.G.; West, A.E.; Tunnell, S.J.; Clark, J.E.; Parsons, J.L.; Engle, D.M.; Hellgren, E.C.; Spears, J.D.H.; Bulter, C.E.; Leslie, D.M. Jr. 2005. **Ecosystem stress from chronic exposure to low levels of nitrate.** EPA/600/R-05/087. Cincinnati, OH: U.S. Environmental Protection Agency, National Risk Management Research Laboratory. 35 p.
- Jovan, S. 2008. **Lichen bioindication of biodiversity, air quality, and climate: baseline results from monitoring in Washington, Oregon, and California.** Gen. Tech. Rep. PNW-GTR-737. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 56 p.
- Jovan, S.; McCune, B. 2005. **Air quality bioindication in the greater Central Valley of California with epiphytic macrolichen communities.** *Ecological Applications*. 15(5): 1712-1726.

- Kelly, V.R.; Lovett, G.M., Weathers, K.C.; G.E. Likens. 2005. **Trends in atmospheric ammonium concentrations in relation to atmospheric sulfate and local agriculture.** *Environmental Pollution*. 135: 363-369.
- Kleijn, D.; Bekker, R.M.; Bobbink, R.; de Graaf, M.C.C.; Roelofs, J.G.M. 2008. **In search for key biogeochemical factors affecting plant species persistence in heathlands and acidic grasslands: a comparison of common and rare species.** *Journal of Applied Ecology*. 45: 680-687.
- Knops, J.M.H; Nash, T.H. III; Boucher, V.L.; Schlesinger, W.L. 1991. **Mineral cycling and epiphytic lichens: implications at the ecosystem level.** *Lichenologist*. 23: 309-321.
- Krupa, S.V. 2003. **Effects of atmospheric ammonia (NH₃) on terrestrial vegetation: a review.** *Environmental Pollution*. 124: 179-221.
- Kytöviita, M.-M.; Crittenden, P.D. 2007. **Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*.** *Annals of Botany*. 100: 1537-1545.
- Lafrancois, B.M.; Nydick, K.R.; Johnson, B.M.; Baron, J.S. 2004. **Cumulative effects of nutrients and pH on the plankton of two mountain lakes.** *Canadian Journal of Fisheries and Aquatic Science*. 61: 1153-1165.
- Latimer J.S.; Rego, S.A. 2010. **Empirical relationship between eelgrass extent and predicted watershed-derived nitrogen loading for shallow New England estuaries.** *Estuarine, Coastal and Shelf Science*. 90: 231-240.
- LeBauer, D.S.; Treseder, K.K. 2008. **Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed.** *Ecology*. 89(2): 371-379.
- Lehmann, C.M.B.; Bowersox, V.C.; Larson, S.M. 2005. **Spatial and temporal trends of precipitation chemistry in the United States, 1985-2002.** *Environmental Pollution*. 135: 347-361.
- Lilleskov, E.A. 1999. **Decline of above- and belowground ectomycorrhizal fungal diversity over an atmospheric nitrogen deposition gradient near Kenai, Alaska.** Ithaca, NY: Cornell University. 198 p. Ph.D. dissertation.
- Lilleskov, E.A. 2005. **How do composition, structure, and function of mycorrhizal fungal communities respond to nitrogen deposition and ozone exposure?** In: Dighton, J.; White, J.F.; Oudemans, P., eds. *The fungal community: its organization and role in the ecosystem*. Boca Raton, FL: Taylor and Francis: 769-801.
- Lilleskov, E.A.; Fahey, T.J.; Horton, T.R.; Lovett, G.M. 2002. **Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska.** *Ecology*. 83: 104-115.
- Lilleskov, E.A.; Fahey, T.J.; Lovett, G.M. 2001. **Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient.** *Ecological Applications*. 11: 397-410.
- Lilleskov, E.A.; Wargo, P.M.; Vogt, K.A.; Vogt, D.J. 2008. **Mycorrhizal fungal community relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition gradient in the northeastern US.** *Canadian Journal of Forest Research*. 38: 1260-1266.
- Liu, L.; Greaver, T.L. 2009. **A review of nitrogen enrichment effects on three biogenic GHGs: The CO₂ sink may be largely offset by stimulated N₂O and CH₄ emission.** *Ecology Letters*. 12: 1103-1117.
- Lovett, G.M.; Tear, T.H. 2008. **Threats from above: Air pollution impacts on ecosystems and biological diversity in the eastern United States.** The Nature Conservancy and the Cary Institute of Ecosystem Studies. www.nature.org/wherewework/northamerica/states/maryland (Accessed May 12, 2010).

- Lovett, G.M.; Tear, T.; Evers, D.; Findlay, S.E.G.; Cosby, B.J.; Dunscomb, J.; Driscoll, C.; K.C. Weathers. 2009. **Effects of air pollution on ecosystems and biological diversity in the eastern United States.** *Annals of the New York Academy of Sciences.* 1162: 99-135.
- Makkonen, S.; Hurri, R.S.K.; Hyvarinen, M. 2007. **Differential responses of lichen symbionts to enhanced nitrogen and phosphorus availability: An experiment with *Cladina stellaris*.** *Annals of Botany.* 99: 877-884.
- Maser, Z.; Maser, C.; Trappe, J.M. 1985. **Food habits of the northern flying squirrel (*Glacomys sabrinus*) in Oregon.** *Canadian Journal of Zoology.* 63: 1084-1088.
- McCune, B.; Grenon, J.; Mutch, L.S.; Martin, E.P. 2007. **Lichens in relation to management issues in the Sierra Nevada national parks.** *Pacific Northwest Fungi.* 2: 1-39.
- McCune, B.M.; Geiser, L.H. 2009. **Macrolichens of the Pacific Northwest. 2nd Edition.** Corvallis, OR: Oregon State University Press. 400 p.
- McKane, R.B.; Johnson, L.C.; Shaver, G.R.; Nadelhoffer, K.J.; Rastetter, E.B.; Fry, B.; Giblin, A.E.; Kiellandk, K.; Kwiatkowski, B.L.; Laundre, J.A.; Murray, G. 2002. **Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra.** *Nature.* 415(6867): 68-71.
- McNulty, S.G.; Boggs, J.L. 2010. **A conceptual framework: redefining forest soil's critical acid loads under a changing climate.** *Environmental Pollution.* 158: 2053-2058.
- McNulty, S.G.; Boggs, J.; Aber, J.D.; Rustad, L.; Magill, A. 2005. **Red spruce ecosystem level changes following 14 years of chronic N fertilization.** *Forest Ecology and Management.* 219: 279-291.
- McNulty, S.G.; Cohen, E.C.; Myers, J.A.M.; Sullivan, T.J.; Li, H. 2007. **Estimates of critical acid loads and exceedances for forest soils across the conterminous United States.** *Environmental Pollution* 149: 281-292.
- Meixner, T.; Fenn, M. 2004. **Biogeochemical budgets in a Mediterranean catchment with high rates of atmospheric N deposition—importance of scale and temporal asynchrony.** *Biogeochemistry.* 70: 331-356.
- Michel, T.J.; Saros, J.E.; Interlandi, S.J.; Wolfe, A.P. 2006. **Resource requirements of four freshwater diatom taxa determined by in situ growth bioassays using natural populations from alpine lakes.** *Hydrobiologia.* 568: 235-243.
- Miller, A.E.; Bowman, W.D. 2002. **Variation in nitrogen-15 natural abundance and nitrogen uptake traits among co-occurring alpine species: do species partition nitrogen form?** *Oecologia.* 130: 609-616
- Mitchell, R.J.; Truscot, A.M.; Leith, I.D.; Cape, J.N.; van Dijk, N.; Tang, Y.S.; Fowler, D.; Sutton, M.A. 2005. **A study of epiphytic communities of Atlantic oak woods along an atmospheric nitrogen deposition gradient.** *Journal of Ecology.* 93: 482-492.
- Moore, T.; Blodau, C.; Turunen, J.; Roulet, N.; Richard, P.J.H. 2004. **Patterns of nitrogen and sulfur accumulation and retention in ombrotrophic bogs, eastern Canada.** *Global Change Biology.* 11 (2): 256-367.
- NADP (National Atmospheric Deposition Program). 2009. **Atmospheric integrated research monitoring network.** Available at <http://nadp.sws.uiuc.edu/airmon/> (Accessed May 17, 2010).
- NEG/ECP (New England Governors and Eastern Canadian Premiers) Forest Mapping Group. 2003. **Assessment of forest sensitivity to nitrogen and sulfur deposition in New England and Eastern**

- Canada - pilot phase report.** Boston: Conference of the New England Governors and Eastern Canadian Premiers. 16 p. Available at <http://www.ecosystems-research.com/fmi/reports.htm> (Accessed May 24, 2010).
- NRC (National Research Council). 2004. **Air quality management in the United States.** Washington, D.C.: National Academy of Sciences Press. 462 p. Available at <http://www.nap.edu/openbook.php?isbn=0309089328> (Accessed May 12, 2010).
- NRCS (National Resources Conservation Service). 2009. **PLANTS database.** Baton Rouge, LA: U.S. Department of Agriculture, Natural Resources Conservation Service, National Plant Data Center. Available at <http://plants.usda.gov> (Accessed May 12, 2010).
- Nilles, M.A.; Conley, B.E. 2001. **Changes in the chemistry of precipitation in the United States, 1981-1998.** *Water, Air and Soil Pollution*. 130: 409-414.
- Nordin, A.; Strengbom, J.; Ericson, L. 2006. **Responses to ammonium and nitrate additions by boreal plants and their natural enemies.** *Environmental Pollution*. 141: 167-174.
- Nordin, A.; Strengbom, J.; Witzell, J.; Näsholm, T.; Ericson, L. 2005. **Nitrogen deposition and the biodiversity of boreal forests: Implications for the nitrogen critical load.** *Ambio*. 34: 20-24.
- Nydick, K.R.; Lafrancois, B.M.; Baron, J.S.; Johnson, B.M. 2004. **Nitrogen regulation of algal biomass, productivity, and composition in shallow mountain lakes, Snowy Range, Wyoming, USA.** *Canadian Journal of Fisheries and Aquatic Science*. 61: 1256-1268.
- Ollinger, S.V.; Aber, J.D.; Lovett, G.M.; Milham, S.E.; Lathrop, R.G. 1993. **A spatial model of atmospheric deposition for the northeastern US. Ecological Applications**. 3: 459-472.
- Ouimet, R.; Arp, P.A.; Watmough, S.A.; Aherne, J.; Demerchant, I. 2006. **Determination and mapping critical loads of acidity and exceedances for upland forest soils in eastern Canada.** *Water, Air and Soil Pollution*. 172: 57-66.
- Pardo, L.H. 2010. **Approaches for estimating critical loads of N and S deposition for forest ecosystems on U.S. Federal lands.** Gen. Tech. Rep. NRS-71. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. 25 p.
- Poikolainen, J.; Lippo, H.; Hongisto, M.; Kubin, E.; Mikkola, K.; Lindgren, M. 1998. **On the abundance of epiphytic green algae in relation to the nitrogen concentrations of biomonitors and nitrogen deposition in Finland.** *Environmental Pollution*. 102: 85-92.
- Porter, E.; Blett, T.; Potter, D.; Huber, C. 2005. **Protecting resources on federal lands: Implications of critical loads for atmospheric deposition of nitrogen and sulfur.** *BioScience*. 55: 603-612.
- Porter, M.K. 2007. **Regional modeling of nitrogen, sulfur and mercury atmospheric deposition in the Pacific Northwest.** Pullman, WA: Washington State University. 127 p. M.S. thesis.
- Posch, M.; de Smet, P.A.M.; Hettelingh, J.-P.; Downing, R.J., eds. 1995. **Calculation and mapping of critical thresholds in Europe.** Status Report 1995. RIVM Rep. No. 259101004. Bilthoven, Netherlands: National Institute for Public Health and the Environment, Coordination Center for Effects. Available at <http://www.mnp.nl/cce/publ/> (Accessed May 12, 2010).
- Posch, M.; de Smet, P.A.M.; Hettelingh, J.-P.; Downing, R.J., eds. 2001. **Modelling and mapping of critical thresholds in Europe.** Status report 2001. RIVM Rep. No. 2591010xx. Bilthoven, The Netherlands: National Institute for Public Health and the Environment, Coordination Center for

- Effects. Available at <http://www.mnp.nl/cce/publ/> (Accessed May 12, 2010).
- Posch, M.; Hettelingh, J.-P.; Sverdrup H.U.; Bull, K. 1993. **Guidelines for the computation and mapping of critical loads and exceedances of sulphur and nitrogen in Europe.** In: Downing, R.J.; Hettelingh, J.-P.; de Smet, P.A.M., eds. Calculation and mapping of critical loads in Europe. CCE Status report 1993. RIVM Rep. No. 259101003. Bilthoven, The Netherlands: National Institute for Public Health and the Environment, Coordination Center for Effects. Available at <http://www.mnp.nl/cce/publ/> (Accessed May 12, 2010).
- Pypker, T.G. 2004. **Influence of canopy structure and epiphytes on the hydrology of Douglas-fir forests.** Corvallis, OR: Oregon State University. 180 p. Ph.D. Thesis.
- Rabalais, N.N. 2002. **Nitrogen in aquatic systems.** *Ambio*. 31: 102-112.
- Rao, L.E.; Allen, E.B. 2010. **Combined effects of precipitation and nitrogen deposition on native and invasive winter annual production in California deserts.** *Oecologia*. 62: 1035-1046.
- Rao, L.E.; Allen, E.B.; Meixner, T. 2010. **Risk-based determination of critical nitrogen deposition loads for fire spread in southern California deserts.** *Ecological Applications*. 20: 1320-1335.
- Rao, L.E.; Parker, D.R.; Bytnerowicz, A.; Allen, E.B. 2009. **Nitrogen mineralization across an atmospheric nitrogen deposition gradient in southern California deserts.** *Journal of Arid Environments*. 73: 920-930.
- Rocheftort, L; Vitt, D.H.; Bayley, S.E. 1990. **Growth, production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions.** *Ecology*. 71(5): 1986-2000.
- Rockström, J.; Steffen, W.; Noone, K.; Persson, Å; Chapin, F.S. III; Lambin, E.F.; Lenton, T.M.; Scheffer, M.; Folke, C.; Schellnhuber, H.J.; Nykvist, B.; de Wit, C.A.; Hughes, T.; van der Leeuw, S.; Rodhe, H.; Sörlin, S.; Snyder, P.K.; Costanza, R.; Svedin, U.; Falkenmark, M.; Karlberg, L.; Corell, R.W.; Fabry, V.J.; Hansen, J.; Walker, B.; Liverman, D.; Richardson, K.; Crutzen, P.; Foley, J.A. 2009. **A safe operating space for humanity.** *Nature*. 461: 472-475.
- Rueth, H.M.; Baron, J.S. 2002. **Differences in Engelmann spruce forest biogeochemistry east and west of the Continental Divide in Colorado, USA.** *Ecosystems*. 5: 45-57.
- Rueth, H.M.; Baron, J.S.; Allstott, E.J. 2003. **Responses of Engelmann spruce forests to nitrogen fertilization in the Colorado Rocky Mountains.** *Ecological Applications*. 13: 664-673.
- Saros, J.E.; Michel, T.J.; Interlandi, S.J; Wolfe, A.P. 2005. **Resource requirements of *Asterionella formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: implications for recent phytoplankton community reorganizations.** *Canadian Journal of Fisheries and Aquatic Science*. 62: 1681-1689.
- Schaberg, P.G.; DeHayes, D.H.; Hawley, G.J.; Murakami, P.F.; Strimbeck, G.R.; McNulty, S.G. 2002. **Effects of chronic N fertilization on foliar membranes, cold tolerance, and carbon storage in montane red spruce.** *Canadian Journal of Forest Research*. 32: 1351-1359.
- Sickman, J.O.; Melack, J.M.; Stoddard, J.L. 2002. **Regional analysis of inorganic nitrogen yield and retention in high-elevation ecosystems of the Sierra Nevada and Rocky Mountains.** *Biogeochemistry*. 57: 341-374.
- Slootweg, J.; Posch, M.; Hettelingh, J.-P., eds. 2007. **Critical loads of nitrogen and dynamic modelling: CCE Progress Report 2007.** MNP Report 500090001. Bilthoven, The Netherlands: Netherlands Environmental Assessment Agency, Coordination Centre for Effects. 201 p. Available at

- <http://www.rivm.nl/en/themasites/cce/publications/cce-progress-report-2007/index.html> (Accessed March 30, 2011).
- Stevens, C.J.; Dise, N.B.; Mountford, J.O.; Gowing, D.J. 2004. **Impact of nitrogen deposition on the species richness of grasslands.** *Science*. 303: 1876-1879.
- Strengbom, J.; Walheim, M.; Näsholm, T.; Ericson, L. 2003. **Regional differences in the occurrence of understory species reflect nitrogen deposition in Swedish forests.** *Ambio*. 32: 91-97.
- Sullivan, T.J.; Cosby, B.J.; Tonnessen, K.A.; Clow, D.W. 2005. **Surface water acidification responses and critical loads of sulfur and nitrogen deposition in Loch Vale watershed, Colorado.** *Water Resources Research*. 41: W01021.
- Suding, K.N.; Gross, K.L.; Houseman, G.R. 2004. **Alternative states and positive feedbacks in restoration ecology.** *Trends in Ecology & Evolution*. 19: 46-53.
- Sutton M.; Reis, S.; Baker; S.M.H., eds. 2009. **Atmospheric Ammonia.** Springer Science. 464 p.
- Theodose, T.A.; Bowman, W.D. 1997. **Nutrient availability, plant abundance, and species diversity in two alpine tundra communities.** *Ecology*. 78: 1861-1872.
- Thomas, R.Q.; Canham, C.D.; Weathers, K.C.; Goodale, C.L. 2010. **Increased tree carbon storage in response to nitrogen deposition in the US.** *Nature Geoscience*. 3: 13-17.
- Tilman, D. 1987. **Secondary succession and the pattern of plant dominance along experimental nitrogen gradients.** *Ecological Monographs*. 57: 189-214.
- Tilman, D. 1993. **Species richness of experimental productivity gradients: How important is colonization limitation.** *Ecology*. 74: 2179-2191.
- Tonnesen, G.; Wang, Z.; Omary, M.; Chien, C.J. 2007. **Assessment of nitrogen deposition: modeling and habitat assessment.** CEC-500-2005-032. Sacramento, CA: California Energy Commission, PIER Energy-Related Environmental Research. 105 p. Available at <http://www.energy.ca.gov/2006publications/CEC-500-2006-032/CEC-500-2006-032.PDF> (Accessed May 12, 2010).
- UBA (UmweltBundesAmt). 2004. **Manual on methodologies and criteria for mapping critical levels/loads and geographical areas where they are exceeded.** Berlin: Federal Environmental Agency (UmweltBundesAmt). Available at <http://www.icpmapping.org> (Accessed May 12, 2010).
- US EPA (U.S. Environmental Protection Agency). 1993. **Air quality criteria for oxides of nitrogen.** Rep. No. EPA/600/8-91/049aF-cF. Research Triangle Park, NC: Office of Health and Environmental Assessment, Environmental Criteria and Assessment Office. 3v.
- US EPA (U.S. Environmental Protection Agency). 2007. **Acid rain and related programs: 2007 progress report.** Washington, DC: U.S. Environmental Protection Agency. Available at <http://www.epa.gov/airmarkets/progress/docs/2007ARPreport.pdf> (Accessed May 12, 2010).
- US EPA (U.S. Environmental Protection Agency). 2008. **Integrated science assessment (ISA) for oxides of nitrogen and sulfur—ecological criteria (final report).** EPA/600/R-08/082F. Research Triangle Park, NC: U.S. Environmental Protection Agency, National Center for Environmental Assessment—RTP Division, Office of Research and Development. Available at <http://cfpub.epa.gov/ncea/cfm/recorddisplay.cfm?deid=201485>.
- USFS (U.S. Forest Service). 2001. **U.S. forest facts and historical trends.** FS-696. Washington, DC: U.S. Department of Agriculture, Forest Service. 20 p.
- van den Berg, L.J.L; Dorland, E.; Vergeer, Philippine; Hart, M.A.C.; Bobbink, R.; Roelofs, J.G.M. 2005.

- Decline of acid-sensitive plant species in heathland can be attributed to ammonium toxicity in combination with low pH.** *New Phytologist*. 166: 551-564.
- van Diepen, L.T.A. 2008. **The role and diversity of arbuscular mycorrhizal fungi in *Acer saccharum* dominated forest ecosystems under natural and N-amended conditions.** Houghton, MI: Michigan Technological University. 99 p. Ph.D. dissertation.
- van Diepen, L.T.A.; Lilleskov, E.A.; Pregitzer, K.S.; Miller, R.M. 2007. **Decline of arbuscular mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions.** *New Phytologist*. 176: 175-183.
- van Herk, C.M.; Mathijssen-Spiekman, E.A.M.; de Zwart, D. 2003. **Long distance nitrogen air pollution effects on lichens in Europe.** *The Lichenologist* 35: 347-359.
- Vitt, D.H.; Wieder, K.; Halsey, L.A.; Turetsky, M. 2003. **Response of *Sphagnum fuscum* to nitrogen deposition: A case study of ombrogenous peatlands in Alberta, Canada.** *The Bryologist*. 1062: 235-245.
- Wallander, H. 1995. **A new hypothesis to explain allocation of dry matter between mycorrhizal fungi and pine seedlings in relation to nutrient supply.** *Plant and Soil*. 169:243-248.
- Weathers, K.C.; Simkin, S.M.; Lovett, G.M.; Lindberg, S.E. 2006. **Empirical modeling of atmospheric deposition in mountainous landscapes.** *Ecological Applications*. 16(4): 1590-1607.
- Wedin, D.A.; Tilman, D. 1996. **Influence of nitrogen loading and species composition on the carbon balance of grasslands.** *Science*. 274: 1720-1723.
- Weiss, S.B. 1999. **Cars, cows, and checkerspot butterflies: Nitrogen deposition and management of nutrient-poor grasslands for a threatened species.** *Conservation Biology*. 13: 1476-1486.
- Whytemare, A.B.; Edmonds, R.L.; Aber, J.D.; Lajtha, K. 1997. **Influence of excess nitrogen deposition on a white spruce (*Picea glauca*) stand in southern Alaska.** *Biogeochemistry*. 38: 173-187.
- Wigand, C.; McKinney, R.A.; Charpentier, M.A.; Chintala, M.M.; Thursby, G.B. 2003. **Relationships of nitrogen loadings, residential development, and physical characteristics with plant structure in New England salt marshes.** *Estuaries*. 26: 1494-1504.
- Williams, M.W.; Tonnessen, K.A. 2000. **Critical loads for inorganic nitrogen deposition in the Colorado Front Range, USA.** *Ecological Applications*. 10(6): 1648-1665.
- Wolfe, A.P.; Baron, J.S.; Cornett, R.J. 2001. **Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the Colorado Front Range (USA).** *Journal of Paleolimnology*. 25: 1-7.
- Wolfe, A.P.; Van Gorp, A.C.; Baron, J.S. 2003. **Recent ecological and biogeochemical changes in alpine lakes of Rocky Mountain National Park (Colorado, USA): a response to anthropogenic nitrogen deposition.** *Geobiology*. 1(2): 153-168.
- Wu, W.; Driscoll, C.T. 2010. **Impact of climate change on three-dimensional dynamic critical load functions.** *Environmental Science and Technology*. 44: 720-726.
- Yoshida, L.C.; Allen, E.B. 2004. **¹⁵N uptake by mycorrhizal *Artemisia californica* and the invasive *Bromus madritensis* of a N-eutrophied shrubland.** *Biology and Fertility of Soil*. 39: 243-248.