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2011

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

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Recommended Citation

Pardo, Linda H., Mark E. Fenn, Christine L. Goodale, Linda H. Geiser, Charles T. Driscoll, Edith B. Allen, Jill S. Baron, Roland Bobbink, William D. Bowman, Christopher M. Clark, Bridget Emmett, Frank S. Gilliam, Tara L. Greaver, Sharon J. Hall, Erik A. Lilleskov, Lingli Liu, Jason A. Lynch, Knute J. Nadelhoffer, Steven S. Perakis, Molly J. Robin-Abbott, John L. Stoddard, Kathleen C. Weathers, and Robin L. Dennis. 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. *Ecological Applications* 21:3049–3082. <http://dx.doi.org/10.1890/10-2341.1>

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Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States

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6 December 2010

Abstract

Human activity in the last century has led to a significant increase in nitrogen (N) emissions and atmospheric deposition. This N deposition has reached a level that has caused or is likely to cause alterations to the structure and function of many ecosystems across the United States. One approach for quantifying the deposition of pollution that would be harmful to ecosystems is the determination of critical loads. A critical load is defined as the input of a pollutant below which no detrimental ecological effects occur over the long-term according to present knowledge.

The objectives of this project were to synthesize current research relating atmospheric N deposition to effects on terrestrial and freshwater ecosystems in the United States, and to estimate associated empirical N critical loads. The receptors considered included freshwater diatoms, mycorrhizal fungi, lichens, bryophytes, herbaceous plants, shrubs, and trees. Ecosystem impacts included: (1) biogeochemical responses 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 volatilization, nitric and nitrous oxide from nitrification and denitrification), and increased N leaching. Individual species, population, and community responses included increased tissue N, physiological and nutrient imbalances, increased growth, altered root:shoot ratios, increased susceptibility to secondary stresses, altered fire regime, shifts in competitive interactions and community composition, changes in species richness and other measures of biodiversity, and increases in invasive species.

The range of critical loads for nutrient N reported for U.S. ecoregions, inland surface waters, and freshwater wetlands is 1-39 kg N ha⁻¹ y⁻¹, spanning the range of N deposition observed over most of the country. The empirical critical loads for N tend to increase in the following sequence for

different life forms: diatoms, lichens and bryophytes, mycorrhizal fungi, herbaceous plants and shrubs, trees.

The critical load approach is an ecosystem assessment tool with great potential to simplify complex scientific information and communicate effectively with the policy community and the public. This synthesis represents the first comprehensive assessment of empirical critical loads of N for major ecoregions across the United States.

Key words: air pollution, atmospheric N deposition, critical nitrogen loads, biodiversity, nitrate leaching, nitrogen saturation, plant nitrogen cycling, natural resource protection, vegetation type conversion

1 **1. Introduction**

2 **1.1 Effects of Nitrogen Deposition on Ecosystems**

3 Human activity in the last century has led to a significant increase in nitrogen (N) emissions
4 and deposition (Galloway et al. 2003). Because of past, and, in some regions, continuing
5 increases in emissions (Nilles and Conley 2001, Lehmann et al. 2005), N deposition has reached
6 a level that has caused or is likely to cause alterations in many ecosystems across the United
7 States. In some ecoregions, the impact of N deposition has been severe, driving altered N cycling
8 and biodiversity. Indicators of altered N cycling include increased N mineralization, nitrification,
9 and nitrate (NO₃⁻) leaching rates, as well as elevated plant tissue N concentration. The eventual
10 outcome of increases in these processes can be N saturation, the series of ecosystem changes that
11 occur as available N exceeds plant and microbial demand (Aber et al. 1989, 1998).

12 As N availability increases there are progressive changes in biotic community structure and
13 composition. For example, in the Mediterranean California ecoregion native plant species in
14 some ecosystems have been replaced by invasive species more productive under elevated N
15 deposition (Weiss 1999, Yoshida and Allen 2004, Fenn et al. 2010, Rao and Allen 2010, Rao et
16 al. 2010). Such shifts in plant community composition and species richness can lead to overall
17 losses in biodiversity and further impair particular threatened or endangered species (Stevens et
18 al. 2004), as has occurred for the checkerspot butterfly (Weiss 1999).

19
20 **1.2 Critical Loads Definition and Previous Uses**

21 One method for evaluating potential impacts of air pollution on ecosystems is critical loads.
22 The critical load is defined as *the deposition of a pollutant below which no detrimental*
23 *ecological effect occurs over the long term according to present knowledge* (UBA 2004). Critical
24 loads have been used broadly in Europe (Posch et al. 1995; Posch et al. 2001) as a tool in the

25 process of negotiating decreases in air pollution. Critical loads have been more widely applied in
26 Canada than in the United States; critical loads have been published for upland forests (Ouimet
27 et al. 2006) and lakes (Dupont et al. 2005) in eastern Canada and included in European
28 assessments (Hettelingh et al. 2008). In the United States (US), critical loads have been
29 calculated for specific regions such as the Northeast (NEC/ECP 2003, Dupont et al. 2005),
30 California (Fenn et al. 2003a, b, 2008), and Colorado (Williams and Tonnessen 2000, Baron
31 2006, Bowman et al. 2006), and, at a coarse scale, the conterminous United States (McNulty et
32 al. 2007).

33 Despite relatively limited use in the US, the critical loads approach is being explored at
34 Federal, state, and international levels as an ecosystem assessment tool with great potential to
35 simplify complex scientific information and communicate effectively with the policy community
36 and the public (Porter et al. 2005, Burns et al. 2008). The critical loads approach can provide a
37 useful lens through which to assess the results of current policies and programs and to evaluate
38 the potential ecosystem-protection value of proposed policy options. Critical loads are used by
39 policymakers to inform the process of setting emissions standards, for assessing emissions
40 control programs, and by natural resource managers as a tool to evaluate the potential impact of
41 new pollution sources (Burns et al. 2008, Environment Canada 2008, Lovett et al. 2009, Porter et
42 al. 2005, US EPA 2007, US EPA 2008). Policymakers and resource managers have used critical
43 loads to establish benchmarks for resource protection and to communicate the impacts of
44 deposition on natural resource conditions.

45 Critical loads have been determined most frequently in the United States for effects of acidity
46 (NEC/ECP 2003, Sullivan et al. 2005), but are also being increasingly used in evaluating impacts
47 of N deposition on ecosystems in terms of excess nutrient N availability, also known as

48 eutrophication (Fenn et al. 2008, 2010). Empirical critical loads are determined from
49 observations of detrimental responses of an ecosystem or ecosystem component to a given,
50 observed N deposition input (Pardo 2010). This level of N deposition is set as the critical load
51 and extrapolated to other similar ecosystems. Empirical critical loads for N are based on
52 measurements from gradient studies, field experiments, or observations (Bobbink et al. 1992,
53 2003, 2010). Other approaches include steady-state mass balance modeling (UBA 2004) and
54 dynamic modeling (de Vries et al. 2010, Slootweg et al. 2007). Steady-state mass balance
55 modeling is based on estimating the net loss or accumulation of nitrogen inputs and outputs over
56 the long term under the assumption that the ecosystem is at steady-state with respect to N inputs.
57 Dynamic models also use a mass balance approach, but consider time-dependent processes and
58 require detailed data sets for parameterization and testing (Belyazid et al. 2006, de Vries et al.
59 2007).

60 The empirical approach has the advantage that it is based on measurable physical evidence of
61 ecosystem responses to N inputs; however, the method will overestimate the critical load (set it
62 too high) if the system has not reached steady state, i.e., if a similar response would occur at a
63 lower deposition level over a longer period because of cumulative dose effects. The only way to
64 determine this empirically is to study the system over a longer time period. Steady-state mass
65 balance approaches have the advantage over the empirical approach of being less likely to
66 overestimate the critical load. In the United States, the uncertainty associated with steady-state
67 mass balance approaches is high because data are not available to quantify the terms in the mass
68 balance equations accurately. Indeed, our empirical critical loads synthesis may be useful in
69 defining the acceptable critical thresholds for application in steady-state mass balance critical
70 loads calculations.

71 Dynamic models for critical loads of N in the United States have been applied on a limited
72 basis (Wu and Driscoll 2010). For dynamic modeling of nutrient N critical loads, empirical
73 critical loads and other response data are essential: the current data for the United States on
74 ecosystem N responses have not been sufficient to develop, parameterize, and test dynamic
75 models that characterize the range of responses that nutrient N has on ecosystem structure and
76 function (for example, changes in biodiversity). Dynamic models are necessary in order to
77 depict the time-dependent response of ecosystems to different levels of N deposition, but the
78 models are only as good as the data upon which they are based. Thus, empirical critical loads
79 currently provide a uniquely valuable approach for assessing the risk of harm to ecosystems in
80 the United States. This synthesis is a first step towards that end by indicating which data are
81 available for key ecosystems and where dynamic modeling could most profitably be applied in
82 the United States after further data collection.

83

84 **1.3 Objectives**

85 Our recent publication (Pardo et al. in press e) synthesized current research relating
86 atmospheric N deposition to effects on terrestrial and freshwater ecosystems in the United States
87 and quantified empirical critical loads for atmospheric N deposition, with one chapter devoted to
88 each of twelve major ecoregions. Our objectives for this paper were to synthesize empirical
89 critical loads for N reported for all the ecoregions of the United States, compare critical loads by
90 life form or ecosystem compartment (mycorrhizal fungi, lichens, herbaceous species, and
91 trees/forest ecosystems) across all ecoregions, discuss the abiotic and biotic factors that affect the
92 critical loads, and compare critical loads in the United States to those for similar

93 ecoregions/ecosystems in Europe. Finally, we discuss the significance of these findings, and the
94 highest priorities for future research.

95

96 **2. Approach**

97 For this synthesis, we reviewed studies of responses to N inputs (Pardo et al. in press e) for
98 U.S. ecoregions as defined by the Commission for Environmental Cooperation (CEC) Level I
99 ecoregions map for North America (CEC 1997; Figure 1; Robin-Abbott and Pardo in press). We
100 identified the receptor of concern (organism or ecosystem compartment), the response of
101 concern, the critical threshold value for that response, and the criteria for setting the critical load
102 and extrapolating the critical load to other sites or regions. These methods are described in detail
103 in Pardo et al. (in press d).

104 The receptors evaluated included freshwater diatoms, mycorrhizal fungi and other soil
105 microbes, lichenized fungi (henceforth lichens), bryophytes, herbaceous plants, shrubs, and trees.
106 Ecosystem impacts included: (1) biogeochemical responses and (2) individual species,
107 population, and community responses. Biogeochemical responses included increased N
108 mineralization and nitrification (and N availability for plant and microbial uptake), increased
109 gaseous N losses (ammonia volatilization, nitrous oxide from nitrification and denitrification),
110 and increased N leaching. Individual species, population and community responses included
111 increased tissue N concentration, physiological and nutrient imbalances, altered growth, altered
112 root:shoot ratios, increased susceptibility to secondary stresses, altered fire regimes, changes in t
113 species abundance, shifts in competitive interactions and community composition (including
114 shifts within and across diatom, bacterial, fungal, or plant taxa groups), and changes in species
115 richness and other measures of biodiversity and increases in invasive species.

116 We considered N addition, N deposition gradient, and long-term monitoring studies in
117 order to evaluate ecosystem response to N deposition inputs. Most of these studies were not
118 designed to quantify critical loads, which presented some challenges. We afforded greater weight
119 to long-term fertilization studies (5-10 years) than to short-term studies, and single-dose forest
120 fertilization studies exceeding 50 kg N ha⁻¹ were generally not considered, although lower dose
121 short-term studies were considered when other observations were limited. When studies were
122 designed in order to determine critical loads, the addition levels generally depicted modest
123 increases above ambient deposition; and were more likely to have smaller increments between
124 the treatment levels; multiple (3+) treatment levels; and, ideally, treatments spanning the critical
125 load. In such cases, estimates of the critical load are made with greater certainty than with other
126 approaches. Nitrogen gradient studies implicitly include longer-term exposure to pollutants and
127 therefore are more likely than N manipulation studies to depict conditions that are near steady-
128 state with respect to ambient N inputs. Long-term monitoring studies sometimes offer the
129 opportunity to observe changes over time in response to increasing or elevated N deposition
130 inputs. We estimated critical loads based on data from >3200 sites (Figure 2).

131 In general, we determined the critical load based on the observed response pattern. In some
132 cases, there was a clear dose-response relationship where the response changed above a certain
133 threshold. A critical threshold is the value of a response parameter which represents an
134 unacceptable condition. The critical threshold is also referred to as the critical limit (UBA 2004).
135 In other cases, when response to increasing N was more linear, we estimated the “pristine” state
136 of N deposition and the deposition that corresponded to a departure from that state. The criteria
137 for setting critical loads are discussed in detail in Pardo et al. (in press d).

138

139 2.1 Deposition

140 Total N emissions have increased significantly since the 1950s (Galloway 1998, Galloway et
141 al. 2003). As S deposition has declined in response to regulation, the rate of N deposition relative
142 to S deposition has increased since the 1980s (Driscoll et al. 2003) followed by a general
143 decrease in NO_x emissions from electric utilities since the early 2000s. More recently, the
144 relative proportion of NH_x (NH₄⁺ + NH₃) to NO_x (NO + NO₂) emissions has also increased for
145 many areas of the United States (Kelly et al. 2005, Lehmann et al. 2005). Deposition at sites
146 included in this analysis (Weathers and Lynch in press) was quantified by the Community
147 Multiscale Air Quality (CMAQ) model v.4.3 (hereafter CMAQ 2001 model; which uses 2001
148 reported data) (Byun and Ching 1999, Byun and Schere 2006) simulations of wet + dry
149 deposition of N species (Figure 2) and was used to calculate exceedance. Exceedance of the
150 critical load is defined as the current deposition minus the critical load; when exceedance is
151 greater than zero, the ecosystem is susceptible to harmful ecological effects. Exceedance is
152 useful in communicating the extent of risk to ecosystems under current and future deposition
153 scenarios.

154 We rarely had data to distinguish biotic or ecosystem response to reduced forms (NH_x)
155 versus oxidized forms (NO_y) of N. There is some evidence that for some species, reduced forms
156 of N may have more substantial impacts than oxidized N (Bobbink et al. 2003; Kleijn et al.
157 2008). This differential response may be due to direct toxicity of gaseous ammonia (NH₃; Krupa
158 2003) or the toxicity to some plant species (or their mycorrhizal fungi) of high levels of
159 ammonium (NH₄⁺) in soil, but can also be a result of soil acidification which occurs when NH₄⁺
160 is nitrified (van den Berg et al. 2005). Lichens in the California Central Valley (Jovan and
161 McCune 2005) have been shown to be particularly sensitive to total reduced N (i.e. NH_x). Across

162 Europe, lichens responded particularly to NH_3 and to a lesser extent NH_4^+ (Cape et al. 2009a,
163 Sutton et al. 2009). Much of the research on NH_3 effects evaluates the response to concentration
164 of NH_3 in air, which would be used for determining the critical level of NH_3 rather than the
165 critical load. This is an important distinction: the critical level is the atmospheric concentration
166 above which adverse effects to sensitive vegetation may occur (UBA 2004). Differences in
167 uptake rates and preference for NH_4^+ versus NO_3^- across different plant taxa (Falkengren-Grerup
168 1995, McKane et al. 2002, Miller and Bowman 2002, Nordin et al. 2006) lead to differences in
169 sensitivity to NH_x (Krupa 2003) and NO_y . Importantly, not all species are more sensitive to NH_x
170 than NO_y ; these responses vary by species and functional type. Some species are more sensitive
171 to increases in NO_y , as was demonstrated for boreal forests (Nordin et al. 2006).

172 In order to quantify the critical load, we generally used the deposition reported in the
173 publication or, when that was not available, we used modeled deposition (e.g., CMAQ, ClimCalc
174 (Ollinger et al. 1993), National Atmospheric Deposition Program (NADP; NADP 2009) maps).
175 The different forms of N deposition included in this assessment were: wet, bulk, wet+dry,
176 throughfall, and total (wet+dry+cloud/fog) inorganic N deposition. Total N deposition was
177 considered the most appropriate value to use in evaluating ecosystem responses; however, in
178 many studies this information is not available. Throughfall N is generally considered a good
179 surrogate for total N deposition, because it typically does not underestimate total N inputs as
180 much as wet or bulk deposition. However, because of the potential for canopy uptake of N,
181 throughfall is usually considered as a lower-bound estimate of total N deposition. None of the
182 studies included reported inputs of organic N, so this report focuses on responses to inputs of
183 inorganic N.

184 The accuracy of the atmospheric N deposition influences the accuracy of the critical load and
185 exceedance estimates. Several factors contribute to uncertainty in N deposition estimates,
186 including the difficulty of quantifying dry deposition of nitrogenous gases and particles to
187 complex surfaces, and sparse data, particularly for arid, highly heterogeneous terrain (e.g.,
188 mountains), sites with high snowfall or high cloudwater/fog deposition, where N deposition
189 tends to be underestimated. Deposition models cannot account for these kinds of heterogeneity
190 (e.g., Weathers et al. 2006) because the spatial scale (grid size) is typically too coarse to capture
191 topographic and other local influences. These issues are discussed in detail elsewhere (Weathers
192 et al. 2006, Fenn et al. 2008, Weathers and Lynch in press). When more accurate and precise N
193 deposition estimates become available, the data presented in this study may be re-evaluated in
194 order to refine the critical loads estimates.

195

196 **3. Results and Discussion**

197 The range of critical loads for nutrient N reported for the United States ecoregions, inland
198 surface waters, and freshwater wetlands is 1-39 kg N ha⁻¹ y⁻¹ (Table 1). This broad range spans
199 the range of N deposition observed over most of the country (see Weathers and Lynch in press).
200 For coastal wetlands, critical loads are between 50-400 kg N ha⁻¹ y⁻¹. The number of locations for
201 which ecosystem response data were available (Figure 2) for an ecoregion is variable, which
202 impacts the level of certainty of the empirical critical loads estimates. The basis for the critical
203 loads values (Tables 1, 2) is discussed in detail in Pardo et al. (in press e).

204

205 **3.1 Comparison of Critical Load by Receptor across Ecoregions**

206 Because N deposition varies considerably by region and the critical load varies both by
207 region and receptor, we present the critical loads and likely risk of exceedance by receptor.

208

209 **3.1.1 Mycorrhizal fungi**

210 *Background*

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

215 *Response to N*

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

228 Of the two plant-fungal symbioses examined here, mycorrhizal fungi appear to be less
229 sensitive to N deposition than lichens (Tables 3 and 4), presumably because the soil environment
230 buffers these soil fungi from some of the immediate impacts of N deposition, whereas lichens
231 are directly exposed to atmospheric N pollution. Lichens have an advantage as indicators when
232 compared with mycorrhizal fungi because they can be relatively easily inventoried. However, the
233 critical role of mycorrhizal fungi as root symbionts central to plant nutrition and belowground
234 production, as repositories of a large part of the eukaryote diversity in forests, as major
235 components of forest food webs, and as non-timber forest products of high economic value
236 (edible sporocarps) (Amaranthus 1998) provides sufficient impetus to improve our understanding
237 of their response to N deposition.

238 *Critical loads*

239 We reviewed empirical studies on mycorrhizal fungal response to N inputs as the basis
240 for determining empirical critical loads for the United States (Table 3, Figure 3.a). Despite the
241 sparse data, it is clear that N deposition sufficient to elevate inorganic N, and especially NO_3^- ,
242 availability in soils can have measurable effects on mycorrhizal fungi. The data for EMF indicate
243 that N deposition to N-limited conifer forests in the range of 5-10 $\text{kg ha}^{-1} \text{ yr}^{-1}$ can significantly
244 alter community structure and composition and decrease species richness (Dighton et al. 2004,
245 Lilleskov 1999, Lilleskov et al. 2001, 2002, 2008). Similarly, the data for AMF suggest N
246 deposition levels of 7.8-12 $\text{kg ha}^{-1} \text{ yr}^{-1}$ can lead to community changes, declines in spore
247 abundance and root colonization, and changes in community function, based on re-analysis of
248 data from Egerton-Warburton et al. (2001) combined with N deposition data and decreases in
249 fungal abundance (van Diepen et al. 2007, van Diepen et al. 2008) and declines in fungal activity
250 (Egerton-Warburton, unpublished data). The actual threshold for N effects on AMF could be

251 even lower, because high background deposition precludes consideration of sites receiving
252 deposition at or near pre-industrial levels. Therefore, our provisional expert judgment is that
253 critical loads for mycorrhizal diversity for sensitive ecosystem types are 5-10 kg ha⁻¹ yr⁻¹. The
254 uncertainty of this estimate is high, because few studies have been conducted at low N deposition
255 to further refine the critical load. The critical load of N for mycorrhizal fungi, when community
256 change occurs, is often on the order of current N deposition and thus is exceeded across most of
257 the eastern and northern forests and in regions downwind of agricultural and urban emissions in
258 the West (Figure 3.b). The uncertainty associated with the exceedance, like that for the CL, is
259 high.

260 3.1.2 Lichens and Bryophytes

261 *Background*

262 Lichens and bryophytes make substantial contributions to biodiversity. About 4,100
263 lichens and 2,300 bryophytes are known from North America north of Mexico—approximately
264 one forth of vascular plant diversity, which is about 26,600 species (USDA, NRCS 2009).
265 Therefore, critical loads protective of the sensitive lichens and bryophytes help protect biological
266 diversity.

267 *Responses to N*

268 Lichens and bryophytes are among the most sensitive bioindicators of N in terrestrial
269 ecosystems (Blett et al. 2003, Bobbink et al. 2003, Fenn et al. 2003a, Glavich and Geiser 2008).
270 Unlike vascular plants, lichens and bryophytes lack specialized tissues to mediate the entry or
271 loss of water and gases (e.g., waxy epidermis, guard cells, root steele). Thus, they rapidly hydrate
272 and absorb gases, water, and dissolved nutrients during high humidity or precipitation events.
273 However, they dehydrate to a metabolically inactive state quickly as well, making them slow

274 growing and vulnerable to contaminant accumulation. Consequently, the implementation of
275 lichen or bryophyte-derived critical loads may prevent undesired impacts to much of the broader
276 forest ecosystem (McCune et al. 2007). In some cases, alteration of lichen community
277 composition may signal the beginning of a cascade of changes in ecosystem N cycling, which
278 may dramatically alter the structure or function of the ecosystem as a whole. In many cases,
279 changes in lichens may have implications beyond the lichen community. In other cases,
280 alterations in the lichen community may have little impact on the overall structure and function
281 of the ecosystem. It can be difficult to know, at the outset, whether the ultimate consequences of
282 changes indicated by alterations to the lichen community will be large or small for the overall
283 ecosystem over the long term.

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

297 microbiota, lichens and bryophytes form cryptogamic mats important to soil stabilization and
298 fertility.

299 *Critical loads*

300 The critical loads estimated (Pardo et al. in press e) for lichens range from 1-9 kg N ha⁻¹
301 yr⁻¹ (Table 4, Figure 4.a). Although the reported range of critical loads is not as large as the
302 ranges for forests or herbs, the certainty associated with these estimates varies considerably. This
303 is partially because of differences in sampling scheme and intensity. For example in the Pacific
304 Northwest, lichen communities were assessed intensively across wide environmental gradients
305 spanning low to high N deposition on a fine grid over time, yielding highly reliable critical N
306 load estimates (Geiser and Neitlich 2007, Jovan 2008) whereas assessments in the eastern United
307 States are more problematic due to historical and contemporary S and acid deposition. In such
308 cases, where historical information necessary to identify a “pristine” or “clean” state is lacking, it
309 is more difficult to determine the critical load, and the resulting confidence associated with the
310 critical load is low. The critical load of N for lichens, based on the shift in community
311 composition when eutrophs dominate at the expense of oligotrophs, is on the order of current N
312 deposition and thus is exceeded across most of the eastern and northern forests and in many areas
313 downwind of agricultural and urban emissions or at high elevation in the West (Figure 4.b). The
314 uncertainty associated with the exceedance, like that for the CL, is low for the Marine West
315 Coast and Northwest Forested Mountains ecoregions, but high elsewhere.

316 Studies in the Pacific Northwest demonstrate that increasing precipitation allows lichens
317 to tolerate higher N deposition (Geiser and Neitlich 2007, Jovan 2008, Geiser et al. 2010, Pardo
318 et al. in press d). The importance of precipitation volume in the critical load for lichens is likely
319 due to the direct influence of N concentration on lichens, that is, the concentrations of N

320 compounds to which lichens are exposed are more important than total loading (Geiser et al.
321 2010). If such simple models could be tested and confirmed in other regions of the country, the
322 confidence in the critical loads in those regions would improve.

323

324 **3.1.3 Herbaceous Species and Shrubs**

325 *Background*

326 Herbaceous species and shrubs (Table 5, Figure 5) are found in grasslands, shrublands,
327 forests, deserts, and wetlands and comprise the majority of the roughly the 26,600 vascular plant
328 species found in North America north of Mexico (USDA, NRCS 2009).

329 *Response to N*

330 Herbaceous species and some shrubs appear intermediate between cryptogram and tree
331 species in their sensitivity to N deposition, due to specialized tissues that mediate the entry or
332 loss of water and gases compared with cryptograms, and rapid growth rates, shallow rooting
333 systems, and often shorter lifespan compared with trees. Thus, herbaceous species in a forest
334 understory will likely respond more rapidly to changes in N deposition and to a greater degree
335 than the trees that they coexist with. Herbaceous species in alpine or tundra environments will
336 respond later and to a lesser degree than the cryptograms that they coexist with. Herbaceous
337 plants clearly play an important role in those ecosystems in which they are the dominant primary
338 producers (e.g., grasslands, shrublands). In forests, however, the role of the herbaceous
339 community in ecosystem function has a significance that is disproportionate to its low relative
340 biomass. For example, although they represent only ~0.2 percent of standing above-ground
341 biomass, herbaceous understory species produce >15 percent of forest litter biomass and

342 comprise up to 90 percent of forest plant biodiversity, including endangered or threatened
343 species (Gilliam 2007).

344 *Critical loads*

345 The range of critical loads for N for herbaceous species and shrubs across all ecoregions
346 is 3-33 kg N ha⁻¹ yr⁻¹ (Table 5, Figure 5). Although this range is broader than those for lichens or
347 mycorrhizal fungi, many of the critical loads for herbaceous species fall into the range of 5-15 kg
348 N ha⁻¹ yr⁻¹. The uncertainty of these estimates is moderate. The shorter lifespan of some
349 herbaceous species results in a more rapid response to N addition. This is especially relevant for
350 perennials with little N storage or annuals. In grasslands, for example, elevated N deposition
351 often leads to a rapid (1-10 years) increase in herbaceous production and a shift in biomass
352 allocation towards more aboveground tissue. This often decreases light levels at ground surface
353 and decreases the numbers of plant species, primarily of perennials, legumes, and natives (Clark
354 and Tilman 2008, Suding et al. 2004, Tilman 1993). Experimental studies of moderate to long
355 duration (3-10 years) allow determination of the critical load with reasonable certainty. Longer
356 studies (>10 years) would decrease the uncertainty further. In some cases, it can be difficult to
357 determine whether the condition in reference plots or at the low end of a deposition gradient
358 represents a “pristine” condition or whether a site has already been altered by N deposition prior
359 to or at the time of the study. For example, the Watershed Acidification Study at Fernow
360 Experimental Forest, West Virginia (Adams et al. 2006) added 35 kg N ha⁻¹ yr⁻¹ via aerial
361 application in addition to ambient deposition of 15-20 kg N ha⁻¹ yr⁻¹, which has led to changes in
362 understory species composition. Recently, similar changes in understory species composition
363 have occurred on the adjacent reference watershed receiving only ambient atmospheric
364 deposition (Gilliam unpublished data, Gilliam et al. 1996). This pattern suggests that the

365 deposition to the reference watershed currently exceeds the critical load. It is difficult to
366 determine the empirical critical load at sites where ambient deposition exceeds the critical load.
367 Where deposition rates exceed the critical load, empirical measurement of the rate of change of
368 an ecological metric (e.g. plant abundance, diversity, or community composition) over a range of
369 N inputs provides an approach to estimate the N level at which that metric just begins to change
370 (the exceeded critical load) (Bowman et al. 2006).

371 The critical load of N for herbaceous species and herbs, when community change occurs
372 (in some cases with invasives replacing native species), is exceeded across much of the Great
373 Plains and in portions of the Southwest and high elevation and high deposition areas of the other
374 ecoregions (Figure 5.b). The uncertainty associated with the exceedance, like that for the CL,
375 varies.

376

377 **3.1.4 Trees/Forest Ecosystems**

378 *Background*

379 In this section we discuss the responses of trees and the overall biogeochemical responses
380 of forest ecosystems to N inputs (Table 6), excluding the specific responses of mycorrhizal fungi,
381 lichens, or understory herbaceous plants. Forest ecosystems represent about a third of landcover
382 in the United States (FIA 2001) and are significant in many of the ecoregions: Northern, Eastern,
383 Tropical Wet, and Marine West Coast Forests, Northwestern Forest Mountains, and
384 Mediterranean California.

385 *Response to N*

386 In northeastern forests, gradient studies demonstrate that N deposition enhances growth
387 in some fast-growing tree species, including the hardwoods studied with arbuscular mycorrhizal

388 associations, whereas it slows growth in some species (red spruce, red maple), and has no
389 detectable effect on still other species (Thomas et al. 2010). Similarly, N deposition enhances
390 survivorship in a few species (black cherry, red maple, paper birch) and decreases survivorship
391 in others (Thomas et al. 2010). Survivorship under chronic N deposition, and possibly other co-
392 occurring pollutants such as ozone, is often dependent on interactions with other stressors such
393 as pests, pathogens, climate change, or drought (Grulke et al. 2009, McNulty and Boggs 2010).
394 Over the long-term, these differential effects of N deposition on tree growth and survivorship are
395 likely to shift species composition, possibly to more nitrophilic species, similar to patterns seen
396 for organisms with shorter lifespans.

397 We have few data that show a major structural or functional shift in forest ecosystems
398 because of the long response time of trees and forest soils to changes in N inputs and N
399 availability (Table 6). The relatively large pools of organic N in the forest floor, mineral soil, tree
400 biomass, and detritus contribute to the relatively long lag-time in forest ecosystem response to N
401 inputs. Because of the long lag-time in response to N treatments, it can be difficult to determine
402 the actual critical N load for forest ecosystems based on short-term fertilization studies. If a
403 response is observed over a relatively short period of time (i.e. years), it is nearly certain that the
404 critical load is below the total N input at the treatment site and it can be difficult to further
405 constrain the critical load.

406 It is expected that the more complex and interconnected processes in forests will result in
407 a higher critical load, in part because large N storage pools give forest ecosystems a greater
408 capacity to buffer N inputs. In herbaceous plants, too, responses in individual species tend to be
409 observed at lower N inputs than changes in community composition, which are more complex
410 and interconnected (Bowman et al. 2006).

411 *Critical loads*

412 The range of critical loads reported for forest ecosystems is 4-39 kg N ha⁻¹ yr⁻¹ (Table 6,
413 Figure 6.a). The threshold N deposition value which caused increased NO₃⁻ leaching from forest
414 ecosystems into surface water was 8-17 kg N ha⁻¹ yr⁻¹; the lower end of the range representing
415 Northern and Eastern Forests, the upper end representing Mediterranean California mixed
416 conifers (Table 6, Figure 7.a). At 4 kg N ha⁻¹ yr⁻¹ in the Colorado Rockies, increasing [NO₃⁻]
417 was reported in the organic horizon, which suggests incipient N saturation (Rueth and Baron
418 2002).The highest critical loads were reported for Mediterranean California mixed conifer forests
419 for forest sustainability and for soil acidification caused by increased N deposition. These sites
420 experience some of the highest N deposition reported in the United States, up to approximately
421 70 kg N ha⁻¹ yr⁻¹ (Fenn et al. 2008).

422 The critical load is exceeded across much of the eastern forests (Eastern and Northern
423 Forest Ecoregions). The lower end of the critical load range is exceeded for the remaining
424 portions of the eastern forests, as well as portions of the Marine West Coast, Northwest Forested
425 Mountains, and Tropical and Sub-tropical Humid Forest Ecoregions (Figure 6.b).

426

427 **3.1.5 Freshwater and wetland ecosystems**

428 *Background*

429 Freshwater lakes and streams, and wetlands (freshwater and estuarine intertidal) are both
430 ecosystem types that occur in most ecoregions in North America. In freshwater lakes and
431 streams, phytoplankton, or algae that live in the water column, are sensitive to the chemical
432 environment in which they reside, and many species can be used as indicators of the levels of
433 nutrients or acidity because of individual species' preference for specific chemical conditions.
434 Diatoms, unicellular plants that form the base of freshwater food webs, are used in this

435 discussion because there has been more work published on these algae than others, but other
436 types of algae also respond to N deposition (Lafrancois et al. 2004, Michel et al. 2006). Of the
437 wetlands which occur in the conterminous United States, 95 percent are freshwater wetlands and
438 5 percent are estuarine or marine wetlands (USDI FWS 2005). The species composition tends to
439 differ between freshwater and intertidal wetlands, although together they support more than 4200
440 native plant species. Despite the high biodiversity, the effects of N loading are studied in just a
441 few plant species.

442 *Response to N*

443 For the analysis of nutrient N effects to freshwater lakes and streams, we relied on papers
444 and studies that linked aquatic biological and ecological response to atmospheric deposition, but
445 the results are consistent with laboratory or *in situ* dose-response studies and even land use
446 change studies. The productivity of minimally disturbed aquatic ecosystems is often limited by
447 the availability of N, and slight increases in available N trigger a rapid biological response that
448 increases productivity and rearranges algal species assemblages (Nydick et al. 2004, Saros et al.
449 2005). The mechanism for change is alteration of N:P ratios, which can increase productivity of
450 some species at the expense of others (Elser et al. 2009). As with the terrestrial systems
451 described above, the nutrient responses of lakes and streams are most evident where land use
452 change and acidic deposition have been limited, thus most evidence of exceedance of critical
453 loads comes from the western United States (Baron et al. in press). As with terrestrial plants,
454 some diatoms respond rapidly to an increase in available N. An example that has been observed
455 from a number of different lakes of the Rocky Mountains is dominance of two diatoms
456 (*Asterionella formosa* and *Fragilaria crotonensis*) in lakes with higher N, in contrast with the
457 flora of lakes with lower N deposition where there is a more even distribution, thus high

458 biodiversity, of diatoms. Higher trophic levels (zooplankton, macroinvertebrates) may be
459 secondarily affected by N, but further increases in primary, or autotrophic, production will be
460 limited by other nutrients such as P or silica (Si).

461 Both freshwater and estuarine intertidal wetlands tend to be N-limited ecosystems
462 (LeBauer and Tresseder 2008, U.S. EPA 1993). Known responses to N enrichment are generally
463 derived from nutrient-addition studies in the field and observations along gradients of N
464 deposition. A variety of ecological endpoints are evaluated, such as altered soil biogeochemistry,
465 increased peat accumulation, elevated primary production, changes in plant morphology,
466 changes in plant population dynamics, and altered plant species composition (U.S. EPA 2008).
467 In general, the sensitivity of wetland ecosystems to nitrogen is related to the fraction of rainfall
468 (a proxy for atmospheric N deposition) in its total water budget. Most freshwater wetlands, such
469 as bogs, fens, marshes and swamps, have relatively closed water and N cycles, thus are more
470 sensitive to N deposition than intertidal wetlands, such as salt marshes and eelgrass beds
471 (Greaver et al. in press).

472 *Critical loads*

473 In general, critical loads for freshwater lakes and streams tend to be low, because the target
474 organisms are unicellular algae that respond rapidly to changes in their chemical environment.
475 The range of critical loads for eutrophication and acidity is 2-9 kg N ha⁻¹ y⁻¹ (Baron et al. in
476 press); the range reported for terrestrial ecosystems is much broader (Table 1). Critical loads for
477 NO₃⁻ leaching from terrestrial ecosystems ranged from 4-17 kg N ha⁻¹ y⁻¹ (Figure 7a), but many
478 sensitive freshwaters at high altitudes are found above the tree-line where few watershed
479 buffering mechanisms exist due to little vegetation, poorly developed soils, short hydraulic
480 residence time, and steep topography. Numerous hydrological factors including hydraulic

481 residence time, N pool size, and conditions of water saturation affect N loss. These factors
482 influence how rapidly a system exhibits elevated N leaching in response to increased N
483 deposition, and how this increased N availability subsequently influences biota. In general, lakes
484 have relatively rapid N turnover times compared to soil N pools and are at least seasonally well-
485 mixed. They would, thus, be expected to have lower critical loads. Turnover times for N in
486 mineral soil pools can be very long, slowing or buffering changes in soil solution that would
487 affect terrestrial plants. Thus responses by terrestrial plants would not be expected to be as rapid
488 as those of freshwater organisms. The critical load for nitrate leaching is exceeded in portions of
489 the Mediterranean California and the lower end of the critical load range is exceeded for most
490 eastern forest and part of the Great Plains (Figure 7.b).

491 Generally the most sensitive type of wetland to N deposition are freshwater wetlands, with
492 critical loads that range from 2.7-14 kg N ha⁻¹ y⁻¹ (Greaver et al. in press). The non-vascular
493 plant genus *Sphagnum* and the carnivorous pitcher plant are the two species most commonly
494 studied. The critical loads reported for freshwater wetlands (Greaver et al. in press) fall between
495 those reported for inland surface waters (Baron et al. in press) and those reported for terrestrial
496 ecosystems (Pardo et al. in press b). This may be related to the rate of N released by
497 soils/sediment to the ecosystem. The critical load tends to be higher for intertidal wetlands than
498 other types of ecosystems because they have open nutrient cycles which are often strongly
499 affected by N loading sources other than atmospheric deposition. Based on field observations of
500 N loading to plant growth and species composition on salt marsh and eel grass habitat, the
501 critical load ranges between 50-400 kg N ha⁻¹ y⁻¹.

502 3.2 Overview of critical loads across U.S. Ecoregions/summary text

503 Empirical critical loads for N tend to increase in the following sequence for different life
504 forms: diatoms, lichens and bryophytes, mycorrhizal fungi, herbaceous plants and shrubs, and
505 trees. Low-biomass ecosystems (e.g., grasslands, coastal sage scrub, desert) are more sensitive to
506 N-enhanced growth of invasive species (if invasive pressure occurs), leading to vegetation type
507 change. These low-biomass ecosystem types sometimes occur because of warm and dry climatic
508 conditions. Because warmer temperatures often correspond to greater metabolic rates, longer
509 periods of biological activity, greater biomass, and more rapid N cycling, one might expect that
510 the critical load would increase with increasing temperature as has been suggested in Europe
511 (Bobbink et al. 2003). We do not observe such a pattern across U.S. ecoregions in the critical
512 loads reported in this synthesis, but Europe does not have warm and dry deserts with low critical
513 loads as in the U.S. Note, however, that the uncertainty of the critical load estimates varies and
514 is often fairly high, which may make it difficult to discern patterns in critical load values across
515 regions. Moreover, a temperature pattern may be confounded by gradients in deposition quality
516 and quantity, moisture and elevation. Critical loads vary more by receptor and response type than
517 by region. For the same response of a given receptor, the western U.S. has generally similar
518 critical load values to the eastern U.S., with the apparent exception that the critical load for NO_3^-
519 leaching is approximately twice as high in Mediterranean California mixed conifers compared to
520 northeastern forests (Figure 7). In contrast, the critical load for NO_3^- leaching in high elevation
521 catchments in the Colorado Front Range are lowest in the United States, likely attributable to low
522 biological N retention and storage capacity in these steep, rocky catchments (Baron et al. 2000,
523 Williams and Tonnessen 2000, Sickman et al. 2002, Fenn et al. 2003a).

524 In setting critical loads, ideally one would identify an indicator that would allow prediction
525 of future deterioration in ecosystem structure or function before it occurs—an early indicator of
526 ecosystem change. We are not yet able to definitively determine which early responses to N
527 deposition are the best indicators. In some cases, early responses may lead to a cascade of
528 alterations in the N cycle that ultimately affect the function or structure of the ecosystem
529 (Galloway et al. 2003). For example, elevated N inputs may lead to plant nutrient imbalances,
530 which then increase plant susceptibility to inciting stressors such as cold, drought, or pests
531 (Bobbink et al. 1998, Schaberg et al. 2002). This series of responses was observed in a southern
532 Vermont montane red spruce stand, where increased foliar N concentration was associated with
533 decreases in foliar membrane-associated calcium and decreased cold tolerance, which resulted in
534 increased winter injury (Schaberg et al. 2002). Another example of the N cascade (Galloway et
535 al. 2003) is increased soil NO_3^- leaching, which can result in episodic acidification of surface
536 waters, harming fish species (Baker et al. 1996).

537 The magnitude or type of ecosystem change that is unacceptable may vary according to
538 resource management goals or ecosystem services that are valued by a particular stake holder. In
539 a conservation area, for example, any alteration in N cycling may be considered unacceptable,
540 whereas for other land areas, changes of a certain magnitude or scope may be considered
541 acceptable or desirable based on resource use (such as timber harvesting) or other factors. For
542 example, some responses to low levels of elevated N deposition, such as increased plant growth
543 and increased C-sequestration by trees (Thomas et al. 2010) may be considered beneficial where
544 forests are managed for tree growth. Land and resources may be valued for a wide range of
545 purposes, including biodiversity, food and wood production, water quality and quantity, and

546 recreation. Quantification and then valuation of these ecosystem services for each land area of
547 interest is required to fully account for impacts of N deposition.

548 There are several sources of uncertainty in our assessment of empirical critical loads, beyond
549 those associated with atmospheric deposition (see section 2.1). In general, there is a dearth of
550 observations on ecosystem response to inputs near the critical load. We suggest priorities for
551 future research to address these data gaps below. A single study or very few studies have been
552 conducted in some ecoregions. Without extensive, spatially stratified observations, it is not
553 possible to know whether a study site is more or less sensitive than other sites in the ecoregion.
554 The threshold value is best defined by a large number of studies which demonstrate the range of
555 responses observed.

556 Other sources of uncertainty include time lags in the response to N deposition and the effects
557 of multiple stressors, both of which are artifacts of the empirical approach, and, as such, are
558 difficult to address. Because ecosystems do not respond instantaneously to changes in N inputs,
559 there is a time lag associated especially with N addition studies; the magnitude of the time lag is
560 a function of the N residence time and the organisms considered. This time lag increases with
561 lifespan and size of organism; a tree will respond more slowly than an herbaceous annual, for
562 example. Time lags are also a function of the rate of N input, with lower rates of input typically
563 leading to longer time lags before an initial response (Clark and Tilman 2008). Some species
564 adapted to low nutrient supply also tend to respond slowly to N additions (Theodose and
565 Bowman 1997). (Note that, although the time lag may be longer for these low-N-adapted
566 species, they may still be amongst the most sensitive to small N additions).

567 Heterogeneity of responses among species within the same ecosystem may be large, with
568 many species being relatively unresponsive and a few opportunistic species transforming

569 community structure and function. For N gradient studies, it can also be difficult to sort out the
570 impact of other factors which may also vary along the deposition gradient, such as climate,
571 interannual variation in weather, soils, vegetation, disturbances, and other pollutants. On the
572 other hand, because these represent “real-world” conditions—in most locations, multiple
573 stressors co-occur—the critical loads estimated in the presence of these stressors may better
574 protect the ecosystems under the current conditions (Fenn et al. 2008).

575 One would anticipate that as an ecosystem approaches N saturation, smaller increments of
576 additional N might result in reaching a “tipping point”. However, it is important not to confuse
577 *proximity to N saturation* with the actual level of deposition; an ecosystem may be near N
578 saturation when the ambient N deposition is low or when it is high. Thus, while prior exposure to
579 elevated N deposition does push an ecosystem towards N saturation, high ambient deposition
580 does not indicate the ecosystems most sensitive to further inputs—that status is a function of the
581 ecosystem characteristics and the receptor.

582 Another source of uncertainty in empirical relationships is that they are simply field
583 observations of responses to N inputs; often mechanistic explanations are lacking. Empirical
584 observations reflect only research done to date, and, with the exception of N addition studies,
585 only conditions observed to date. Because these factors affect the accuracy of the critical load, it
586 is important to consider the level of uncertainty associated with our estimates of critical loads
587 (Pardo et al. in press d). With more long-term studies and more data on the response of
588 ecosystems to changes in N deposition, confidence in empirical loads will improve, as has
589 occurred in Europe (Bobbink et al. 1992, 2010). In addition, over time, empirical observations
590 will continue to inform dynamic models and improved dynamic models will facilitate
591 understanding of the mechanisms behind field observations.

592

593 **3.3 Factors that affect the Critical Load**

594 One of the objectives of this assessment was to lay the groundwork for further refining and
595 improving estimates of critical loads. To that end, in this section, we discuss some of the factors
596 that affect where the value of the critical load falls within the reported range (Table 2). Abiotic
597 factors which may affect the critical load include elevation, latitude, topographic location,
598 climate (temperature, precipitation, extent and rate of climate change), catchment size, soil type,
599 soil age, soil depth extent of soil cover in high elevation systems, parent material, and hydrologic
600 flowpaths and processes. Disturbance may also play a substantial role, for example, N removal
601 by fire or forest cutting may increase the critical load for nutrient N. A sub-region within an
602 ecoregion may be more sensitive (e.g., the high-elevation Rockies are more sensitive to NO_3^-
603 leaching than high elevation catchments in the Sierra Nevada of California). Biological factors
604 likely to contribute to lower N critical loads include particularly sensitive species (diatoms,
605 lichens, mycorrhizal fungi, certain plants), single species versus community responses, low
606 biomass and low productivity ecosystems, short lifespan of receptor of concern, presence of
607 invasive grasses, and presence of ozone-sensitive species.

608 The factors discussed above provide general guidance in applying critical loads. In order to
609 set a critical load for a given site, the first step would be to determine whether the site of concern
610 is similar to the site/or sites on which the critical load for that ecosystem type is based. Details on
611 the estimation of critical loads are described for Tundra (Nadelhoffer and Geiser, in press), Taiga
612 (Geiser and Nadelhoffer in press), Northern Forests (Pardo et al. in press c), Northwestern
613 Forested Mountains (Bowman et al. in press), Marine West Coast Forests (Perakis et al. in
614 press), Eastern Forests (Gilliam et al. in press), Great Plains (Clark in press), North American

615 Deserts (Allen and Geiser in press), Mediterranean California (Fenn et al. in press), Southern
616 Semi-Arid Highlands (Fenn and Allen in press), Temperate Sierra (Fenn and Geiser in press),
617 Tropical and Subtropical Humid Forests (Hall in press), Wetlands (Greaver et al. in press),
618 Inland surface waters (Baron et al. in press). If the site differs from the sites upon which the
619 critical load is based, Table 2 lists ecoregion-specific factors affecting the critical load that can
620 be useful in adjusting the estimated critical load for a given site.

621 The more we are able to identify and quantify the factors that affect the critical load, the
622 more we move towards a mechanistic understanding of the responses, and the better we are able
623 to extrapolate observations across ecoregions or across different ecosystems within an ecoregion.
624 In some cases, it may be possible to develop simple empirical relationships as a function of one
625 or several variables that allow us to refine our critical loads estimates. For example, for lichens,
626 Geiser et al. (2010) developed simple regression relationships which included precipitation that
627 explain much of the variability in lichen community composition in response to N deposition.
628 These regression models can be used to estimate critical loads in other regions and also can
629 provide an estimate of the uncertainty associated with the critical load. Such models, strongly
630 tied to empirical observations, will prove invaluable in the development of dynamic models for
631 nutrient N critical loads.

632

633 **3.4 Comparison to Critical Loads in Europe**

634 The critical loads for N deposition we report are consistently lower than those reported for
635 Europe, with a few exceptions (Pardo et al. in press). It is difficult to make the comparison
636 between the United States and Europe because the ecosystem classification systems used are not
637 parallel and critical loads are often at different resolution or detail of vegetation classification.

638 Furthermore, the response variables and thresholds values of those variables are not always the
639 same.

640 There are several reasons that critical loads for Europe may be higher than for the United
641 States. One explanation for this pattern is that because of high historic deposition levels, many
642 European systems lack pristine baseline ecosystems as a reference to compare those experiencing
643 elevated N deposition. If the baseline reference sites are already altered by N deposition, then
644 there is no means of estimating critical loads below the altered baseline. This is even more likely
645 to have occurred in regions of Europe where deposition has been very high. For example,
646 European critical loads for lichens were influenced by study sites in Scotland experiencing a
647 deposition gradient from 10-22 kg N ha⁻¹ y⁻¹ from which critical loads were set at 11-18 kg N ha⁻¹
648 y⁻¹ (Mitchell et al. 2005). However, no oligotrophic species were observed, presumably because
649 they were eliminated following initial increases in N deposition earlier in the 20th century. Not
650 surprisingly, this European critical load is higher than any N critical loads for lichens in the
651 United States. In addition, NH₄⁺ inputs tend to be higher and represent a greater proportion of
652 total N inputs in Europe, particularly in past decades. Note that when dry deposition is
653 underestimated in the United States, the critical loads will also be underestimated which would
654 contribute to them being lower than those in Europe (where throughfall is often used to set
655 critical loads). Finally, since a greater proportion of the landscape in Europe, especially forested
656 land, is managed (harvested and planted), this may contribute to European critical loads being
657 higher as N removal by harvesting results in greater N demand and storage during re-
658 establishment of the forest stand.

659 Another possible explanation for the fact that European critical loads are often higher than
660 those reported here is that the response thresholds utilized in Europe are sometimes higher. A

661 key example is lichen community response: when a shift in community composition is
662 considered the threshold of change, the critical loads will be low. Some earlier work in Europe,
663 in contrast, used a different biological threshold--the near extirpation of lichen species—leading
664 to a higher critical load (Bobbink et al. 2003). Another example of higher response thresholds
665 used for setting critical loads in Europe relates to responses at the forest ecosystem level. Using a
666 more sensitive endpoint, such as initial changes in N biogeochemistry interpreted as incipient
667 responses of N saturation, led to a critical load $< 4 \text{ kg N ha}^{-1} \text{ y}^{-1}$ in the Colorado Front Range
668 (Rueth et al. 2003). This is a subtle initial N enrichment response when compared to the
669 magnitude of change (a later stage of N saturation) for the critical loads thresholds in Europe
670 (10-15 kg/ha/yr). Note that critical loads in China are even higher than those in Europe (Duan
671 2009).

672

673 **4. Conclusions**

674 Because most terrestrial and many freshwater ecosystems are N limited under unpolluted
675 conditions, increases in N input to ecosystems are likely to have an impact. Increased N
676 deposition can cause a shift in the processing and fluxes of N along with an array of biological
677 responses caused by N enrichment (function) and can cause significant changes to the physical
678 composition (structure) of ecosystems. The resources most threatened by elevated N deposition
679 include diatoms, lichens, bryophytes, and herbaceous plants. The most significant changes that
680 we are currently observing in the United States in response to elevated N deposition are changes
681 in species composition: losses of N-sensitive species, shifts in dominance, and losses of native
682 species in favor of exotic, invasive species. Shifts in diatom and lichen community composition
683 away from N-intolerant (oligotrophic) species are observed across the country. Alterations in

684 herbaceous species are broadly observed, but are not always clearly documentable because of the
685 long-term pollution inputs and other disturbances (including land-use change) that caused
686 changes prior to the initiation of careful observations.

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

699 Changes in ecosystem structure are linked to changes in ecosystem function. For example,
700 extirpation of lichens can alter food webs by reducing the availability of nesting material for
701 birds, invertebrate habitat, and critical winter forage for mammals, and can also affect nutrient
702 cycling (Cornelissen et al. 2007). In California, where elevated N deposition occurs in arid low-
703 biomass ecosystems (e.g., coastal sage scrub, grassland, desert), N-enhanced growth of invasive
704 species results in major alterations of plant communities, conversion of vegetation type, and
705 increased fire risk, even in areas where fire is normally infrequent (Allen et al. 2009, Rao et al.
706 2010, Fenn et al. 2010).

707 There is also evidence of N deposition contributing to multiple stress complexes, resulting
708 in reduced forest sustainability in California (Grulke et al. 2009) and North Carolina (McNulty
709 and Boggs 2010). In North Carolina, elevated N deposition predisposed a pine ecosystem to a
710 pest outbreak following a drought (McNulty and Boggs 2010). Another example of N deposition
711 interactions with other forest stressors is the observation that increased NO_3^- leaching and
712 nitrification contribute to soil acidification and depletion of available nutrient cations, which
713 have negative effects on tree growth, vigor, and cold tolerance in some forests (Driscoll et al.
714 2001). These types of complex interactions may be difficult to predict, but may intensify the
715 impact of elevated N deposition in concert with other stressors, including climate change. (Wu
716 and Driscoll 2010). Further examples of changes in ecosystem structure and function are
717 observed in coastal areas, where increased N export has led to toxic algal blooms (Rabalais
718 2002). As an example of N deposition effects on trace gas chemistry and climate change, N
719 loading to ecosystems results in increased emissions of N trace gases, such as NO (nitric oxide,
720 an ozone precursor), N_2O (nitrous oxide, a long-lived and powerful greenhouse gas); as well as
721 declines in soil uptake of CH_4 (methane, another long lived and powerful greenhouse gas) (e.g.,
722 Liu and Greaver 2009).

723 This synthesis demonstrates that elevated N deposition has altered ecosystem structure and
724 function across the United States. Empirical critical loads for N provide a valuable approach for
725 evaluating the risk of harm to ecosystems. This approach has been used broadly in Europe
726 (Bobbink et al. 2003, UBA 2004) and has the advantage of being scientifically based on
727 observed responses. This link to actual ecosystem responses is especially beneficial in resource
728 management and policy contexts.

729 Pardo et al. (in press e) provides the first comprehensive assessment of empirical critical
730 loads of N for ecoregions across the United States. It represents an important step toward
731 providing policymakers and resource managers with a tool for ecosystem protection, as was
732 suggested by the National Research Council (NRC 2004).

733

734 **5. Future Research Priorities**

735 The principal knowledge gaps that limit our understanding of N impacts on ecosystems
736 include poor quantification of total N deposition (especially in deposition hotspots), the paucity
737 of long-term, low N fertilization studies and adequate N deposition gradient studies. A higher
738 density of long-term, low N fertilization studies and long-term and larger scale gradient studies
739 across a greater diversity of ecosystem types and extending to regions of low N deposition are
740 necessary in order to develop the dose response curves that would better define the critical load
741 and the associated uncertainty. These studies should examine all of the key receptors defined
742 above, to explicitly test their relative sensitivity to N deposition and suitability as indicators of
743 changes in other system properties. Future research should be directed at evaluating
744 environmental and ecological factors that influence critical loads for ecoregions and quantifying
745 how the critical load varies as key factors change across ecoregions. In the United States, the
746 sparsest datasets are in the tundra, taiga, and desert ecoregions. Other important issues include:

- 747 • the differential response to reduced (NH_x) versus oxidized (NO_x) N inputs. Because some
748 plants are particularly sensitive to NH_x inputs (Krupa 2003) while others are more
749 sensitive to NO_y (Nordin et al. 2006), assembling more comprehensive data about these
750 species-specific responses would allow more accurate assessment of potential risks to
751 ecosystems in relation to the major N emissions sources.

- 752 • impacts on plant biodiversity have not been well described, in part, because of the
753 difficulty of assessing such changes in ecosystems with longer-lived organisms, and, in
754 part, because in many of these ecosystems, the herbaceous plants have been altered by
755 historical N deposition, other pollutants, or habitat alteration.
- 756 • effects of N deposition on forest growth and sustainability. Insufficient data are available
757 to determine critical loads for the effects of increasing N inputs on pest outbreaks,
758 drought, cold tolerance, tree vigor, and multiple stress complexes in general.
- 759 • identification of mechanisms that control plant and ecosystem responses to N deposition.
760 This is a necessary step in refining critical loads estimates, improving their reliability,
761 and laying the groundwork for more complex dynamic models, which are necessary for
762 broad scale assessments, including detailed national maps of empirical critical loads for
763 N.

764 Better integration of improved atmospheric deposition models, empirical and dynamic
765 critical load models, and vegetation cover data layers. From this critical load and critical load
766 exceedance maps should be developed at scales useful for regulatory, policy making, land
767 management, and resource protection purposes.

768

769 **Acknowledgments**

770 This project was funded, in part, by the US-EPA Clean Air Markets Division, DW-12-92196101.
771 Initial work on this project was funded by the US Forest Service Air Resource Management
772 Program. Funding was provided by the UCR Center for Conservation Biology and NSF grant
773 DEB 04-21530. We would also like to thank Amanda Elliot, and Robert Johnson for their
774 assistance in creating deposition and critical loads maps.

775

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777 **Literature Cited**

- 778 Aber, J., McDowell, W., Nadelhoffer, K., Magill, A., Berntson, G., Kamakea, M., McNulty, S.,
779 Currie, W., Rustad, L., Fernandez, I. 1998. Nitrogen saturation in temperate forest
780 ecosystems. *Bioscience*. 48: 921-934.
- 781 Aber, J.D., Goodale, C.L., S.V. Ollinger, M.-L. Smith, A.H. Magill, M.E. Martin, R.A. Hallet,
782 and J.L. Stoddard. 2003. Is nitrogen deposition altering the nitrogen status of Northeastern
783 forests? *Bioscience* 53(4): 375-389.
- 784 Aber, J.D., Nadelhoffer, K.J., Steudler, P., Melillo, J.M. 1989. Nitrogen saturation in northern
785 forest ecosystems. *BioScience*. 39: 378-386.
- 786 Adams, M.B., DeWalle, D.R., Peterjohn, W.T., Gilliam, F.S., Sharpe, W.E., Williard, K.W.J.
787 2006. Soil Chemical Responses to Experimental Acidification Treatments. In: Adams,
788 M.B., DeWalle, D.R., Hom, J.L, eds. *The Fernow Watershed Acidification Study*.
789 Dordrecht, The Netherlands: Springer: 41-69.
- 790 Aldous, A.R. 2002. Nitrogen retention by *Sphagnum* mosses: responses to atmospheric nitrogen
791 deposition and drought. *Canadian Journal of Botany* 80: 721-731.
- 792 Allen, E.B., and Geiser, L.H. In press. North American deserts. In: Pardo, L.H., Robin-Abbott,
793 M.J., Driscoll, C.T., eds. *Assessment of effects of N deposition and empirical critical*
794 *loads for nitrogen for ecoregions of the United States*. USDA Forest Service General
795 Technical Report, xxx pp.
- 796 Allen, E.B., Rao, L.E., Steers, R.J., Bytnerowicz, A., Fenn, M.E. 2009. Impacts of atmospheric
797 nitrogen deposition on vegetation and soils in Joshua Tree National Park. In: Webb,
798 R.H., Fenstermaker, L.F., Heaton, J.S., Hughson, D.L., McDonald, E.V., Miller, D.M.,

799 eds. The Mojave Desert: Ecosystem Processes and Sustainability. Las Vegas: University
800 of Nevada Press. Pp. 78-100.

801 Allen, E.B., Temple, P.J., Bytnerowicz, A., Arbaugh, M.J., Sirulnik, A.G., and Rao, L.E. 2007.
802 Patterns of understory diversity in mixed coniferous forests of southern California
803 impacted by air pollution. The Scientific World Journal. 7(S1): 247-263. DOI
804 10.1100/tsw.2007.72.

805 Amaranthus, M. P. 1998. The importance and conservation of ectomycorrhizal fungal diversity
806 in forest ecosystems: Lessons from Europe and the Pacific Northwest. U S Forest Service
807 General Technical Report PNW QTR-431.

808 Arens, S.J.T., Sullivan, P.F., Welker, J.M. 2008. Nonlinear responses to nitrogen and strong
809 interactions with nitrogen and phosphorus additions drastically alter the structure and
810 function of a high arctic ecosystem. Journal of Geophysical Research-Biogeosciences 113.

811 Baker, J.P., Van Sickle, J., Gagen, C.J., Baldigo, B.P., Bath, D.W., Carline, R.F., DeWalle, D.R.,
812 Kretser, W.A., Murdoch, P.S., Sharpe, W.E., Simonin, H.A., Wigington, P.J. 1996.
813 Episodic acidification of small streams in the northeastern United States: Effects on fish
814 populations. Ecological Applications. 6: 422-437.

815 Baez, S., Fargione, J., Moore, D.I., Collins, S.L., Gosz, J.R. 2007. Atmospheric nitrogen
816 deposition in the northern Chihuahuan desert: Temporal trends and potential consequences.
817 Journal of Arid Environments. 68: 640-651.

818 Barret, J.E., Burke, I.C. 2002. Nitrogen retention in semiarid ecosystems across a soil organic-
819 matter gradient. Ecological Applications. 12: 878-890.

820 Baron, J.S. 2006. Hindcasting nitrogen deposition to determine ecological critical load.
821 Ecological Applications 16(2): 433-439.

822 Baron, J.S., Driscoll, C.T., Stoddard, J.L. In press. Inland surface water. In: Pardo, L.H., Robin-
823 Abbott, M.J., Driscoll, C.T., eds. Assessment of effects of N deposition and empirical
824 critical loads for nitrogen for ecoregions of the United States. USDA Forest Service
825 General Technical Report, xxx pp.

826 Baron, J.S., Ojima, D.S., Holland, E.A., Parton, W.J. 1994. Analysis of nitrogen saturation
827 potential in Rocky Mountain tundra and forest: Implications for aquatic systems.
828 *Biogeochemistry*. 27: 61-82.

829 Baron, J.S., Rueth, H.M., Wolfe, A.M., Nydick, K.R., Allstott, E.J., Minear, J.T., Moraska, B.
830 2000. Ecosystem responses to nitrogen deposition in the Colorado Front Range.
831 *Ecosystems*. 3: 352-368.

832 Belyazid S. Westling, O. Sverdrup, H. 2006. Modelling changes in forest soil chemistry at 16
833 Swedish coniferous forest sites following deposition reduction. *Environmental Pollution*
834 144:596-609.

835 Berryman, S., Geiser, L., Brenner, G. 2004. Depositional gradients of atmospheric pollutants in
836 the Athabasca Oil Sands region, Alberta, Canada: an analysis of lichen tissue and lichen
837 communities. Lichen Indicator Pilot Program 2002-2003. Final Report Submitted to the
838 Terrestrial Environmental Effects Monitoring (TEEM) Science Sub-committee of the
839 Wood Buffalo Environmental Association (WBEA). February 25, 2004.

840 Berryman, S., Straker, J. 2008. Nitrogen Loading and Terrestrial Vegetation – Assessment of
841 Existing Regional Monitoring and Recommendations. Report prepared for the Cumulative
842 Environmental Management Association NO_x-SO₂ Management Working Group and
843 Eutrophication Task Group. Submitted by CE Jones and Associates, Sidney, BC.

844 Blett, T., Geiser, L., Porter, E. 2003. Air Pollution-Related Lichen Monitoring in National Parks,
845 Forests, and Refuges Guidelines of Studies Intended for Regulatory and Management
846 Purposes. Report NPS D2292.

847 Bobbink, R., Ashmore, M., Braun, S., Flückinger, W., van den Wyngaert, I.J.J. 2003. Empirical
848 nitrogen critical loads for natural and semi-natural ecosystems: 2002 update. In:
849 Achermann, B., Bobbick, R., eds. Empirical critical loads for nitrogen. Environmental
850 Documentation No. 164. Berne, Switzerland: Swiss Agency for the Environment, Forests,
851 and Landscape: 43-107.

852 Bobbink R., Boxman D., Fremstad E., Heil G., Houdijk A., Roelofs J. 1992. Critical loads for
853 nitrogen eutrophication of terrestrial and wetland ecosystems based upon
854 changes in vegetation and fauna. In: Grennfelt and Thörnelöf, eds. Critical loads for nitrogen.
855 Nord 41:111-159.

856 Bobbink, R., Hicks, K., Galloway, J.N., Spranger, T., Alkemade, R., Ashmore, M., Bustamante,
857 M.M.C., Cinderby, S., Davidson, E.A., Dentener, F., Emmett, B., Erisman, J.-W., Fenn,
858 M., Gilliam, F., Nordin, A., Pardo, L., de Vries, W. 2010. Global assessment of nitrogen
859 deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications.

860 Bobbink, R., Hornung, M., Roelofs, J.G.M.. 1998. The effects of air-borne nitrogen pollutants on
861 species diversity in natural and semi-natural European vegetation. Journal of Ecology 86:
862 738.

863 Boonpragob, K., Nash, T.H. III, Fox, C.A. 1989. Seasonal deposition patterns of acidic ions and
864 ammonium to the lichen *Ramalina menziesii* Tayl. in southern California. Environ. Exp.
865 Bot., 29: 187-197.

866 Bowman, W.D., Baron, J.S., Geiser, L.H., Fenn, M.E., Lilleskov, E.A. In press. Northwestern
867 Forested Mountains. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T., eds. Assessment
868 of effects of N deposition and empirical critical loads for nitrogen for ecoregions of the
869 United States. USDA Forest Service General Technical Report, xxx pp.

870 Bowman, W.D., Larson, J.R., Holland, K., Wiedermann, M., Nieves, J. 2006. Nitrogen critical
871 loads for alpine vegetations and ecosystem response- are we there yet? Ecological
872 Applications. 16(3): 1183-1193.

873 Bowman, W.D., Larson, J.R., Holland, K., Wiedermann, M., Nieves, J. 2006. Nitrogen
874 critical loads for alpine vegetations and ecosystem response- are we there yet? Ecological
875 Applications. 16(3): 1183-1193.

876 Breiner, J., Gimeno, B.S., Fenn, M. 2007. Calculation of theoretical and empirical nutrient N
877 critical loads in the mixed-conifer ecosystems of southern California. The Scientific World
878 Journal. 7(S1): 198-205. DOI 10.1100/tsw.2007.65.

879 Burns, D.A., Blett, T., Haeuber, R., Pardo, L.H. 2008. Critical loads as a policy tool for
880 protecting ecosystems from the effects of air pollutants. Frontiers in Ecology and the
881 Environment doi:10.1890/070040.

882 Byun, D.W., Ching, J.K.S., eds. 1999. Science algorithms of the EPA models-3 community
883 multiscale air quality model (CMAQ) modeling system. Washington, DC: U.S.
884 Environmental Protection Agency, Office of Research and Development, EPA/600/R-
885 99/030. <http://www.epa.gov/asmdnerl/CMAQ/CMAQscienceDoc.html>.

886 Byun, D., and Schere, K.L. 2006. Review of the governing equations, computational algorithms,
887 and other components of the Models-3 Community Multiscale Air Quality (CMAQ)
888 modeling system. Applied Mechanics Reviews. 59: 51-77.

889 Caffrey, J.M., Murrell, M.C., Wigand, C., McKinney, R. 2007. Effect of nutrient loading on
890 biogeochemical and microbial processes in a New England salt marsh. *Biogeochemistry*
891 82: 251-264.

892 Cape, J.N., van der Eerden, L.J., Sheppard, L.J., Leith, I.D, Sutton, M.A. 2009a. In: Sutton M.,
893 Reis, S., Baker, S.M.H., eds. *Atmospheric Ammonia*. Springer Science, 15-40.

894 Cape, J.N., van der Eerden, L.J., Sheppard, L.J., Leith, I.D. and Sutton, M.A. 2009b. Evidence
895 for changing the critical level for ammonia. *Environ. Pollut.* 157:1033-1037.

896 Clark, C. M. In press. Great Plains. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T., eds.
897 *Assessment of effects of N deposition and empirical critical loads for nitrogen for*
898 *ecoregions of the United States*. USDA Forest Service General Technical Report, xxx pp.

899 Clark, C. M., and Tilman, D. 2008. Loss of plant species after chronic low-level nitrogen
900 deposition to prairie grasslands. *Nature* 451:712-715.

901 Clark, C.M., Hobbie, S., Venterea, R., Tilman, D. 2009. Long-lasting effects on N cycling 12
902 years after treatments cease despite minimal N retention. *Global Change Biology* in press.

903 Clark, J.E., Hellgren, E.C., Jorgensen, E.E., Leslie, D.M. 2005. Population dynamics of harvest
904 mice (*Reithrodontomys fulvescens* and *R. montanus*) across a nitrogen-amended old field.
905 *American Midland Naturalist*. 154:240-252.

906 Clark, J.E., Hellgren, E.C., Jorgensen, E.E., Tunnell, S.J., Engle, D.M., Leslie, D.M. 2003.
907 Population dynamics of hispid cotton rats (*Sigmodon hispidus*) across a nitrogen-amended
908 landscape. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*. 81:994-1003.

909 Commission for Environmental Cooperation. 1997. *Ecological Regions of North America*.
910 *Toward a Common Perspective*. 71 pp.
911 http://www.cec.org/pubs_docs/documents/index.cfm?id=344.

912 Cornelissen, J.H.C., Lang, S.I., Soudzilovskaia, N.A., During, H.J. 2007. Comparative
913 Cryptogam Ecology: A Review of Bryophyte and Lichen Traits that Drive
914 Biogeochemistry. *Annals of Botany* 99: 987–1001.

915 De Vries, W., Kros, J., Reinds, G.J., Wamelink, W., van Dobben, H., Bobbink, R., Emmett, B.,
916 Smart, S., Evans, C., Schlutow, A., Kraft, P., Belyazid, S., Sverdrup, H., Hinsberg, A. van,
917 Posch, M., Hettelingh, J.P. 2007. Developments in modelling critical nitrogen loads for
918 terrestrial ecosystems in Europe. Report 1382. Alterra Wageningen UR, Wageningen, The
919 Netherlands.

920 De Vries, W., Wamelink, W., van Dobben, H., Kros, H., Reinds, G.J., Mol-Dijkstra, J., Smart,
921 S., Evans, C., Rowe, E., Belyazid, S., Sverdrup, H., van Hinsberg, A., Posch, M.,
922 Hettelingh, J.-P., Spranger, T., Bobbink, R. 2010. Use of dynamic soil-vegetation models
923 to assess impacts of nitrogen deposition on plant species composition: an overview.
924 *Ecological Applications*.

925 Dighton, J., Tuininga, A.R., Gray, D.M., Huskins, R.E., Belton, T. 2004. Impacts of atmospheric
926 deposition on New Jersey pine barrens forest soils and communities of ectomycorrhizae.
927 *Forest Ecology and Management* 201: 131-144.

928 Driscoll, C.T., Lawrence, G.B., Bulger, A.J., Butler, T.J., Cronan, C.S., Eagar, C., Lambert, K.F.,
929 Likens, G.E., Stoddard, J.L., Weathers, K.C. 2001. Acidic deposition in the northeastern
930 United States: Sources and inputs, ecosystem effects, and management strategies.
931 *BioScience* 51: 180-198.

932 Driscoll, C.T., Whitall, D., Aber, J., Boyer, E., Castro, M., Cronan, C., Goodale, C.L., Groffman,
933 P., Hopkinson, C., Lambert, K., Lawrence, G., Ollinger, S. 2003. Nitrogen pollution in the

934 northeastern United States: sources, effects, and management options. *BioScience* 53:357-
935 374.

936 Duan, L. 2009. Empirical Critical Loads of Nitrogen in China. Proceedings from a Workshop on
937 Nitrogen Deposition, Critical Loads, and Biodiversity, Edinburgh, 16-18 November, 2009.

938 Dupont, J., Clair, T.A., Gagnon, C., Jeffries, D.S., Kahl, J.S., Nelson, S., Peckenham, J. 2005.
939 Estimation of critical loads of acidity for lakes in northeastern United States and eastern
940 Canada. *Environmental Monitoring Assessment* 109:275-292.

941 Egerton-Warburton, L. M., and Allen, E.B. 2000. Shifts in arbuscular mycorrhizal communities
942 along an anthropogenic nitrogen deposition gradient. *Ecological Applications*. 10: 484-
943 496.

944 Egerton-Warburton, L.M., Graham, R.C., Allen, E.B., Allen, M.F. 2001. Reconstruction of the
945 historical changes in mycorrhizal fungal communities under anthropogenic nitrogen
946 deposition. *Proceedings of the Royal Society of London*. B268: 2479-2484.

947 Elser, J.J., Anderson, T., Baron, J.S., Bergström, A-K, Kyle, M., Nydick, K.R., Steger, L.,
948 Hessen, D.O. 2009. Shifts in lake N:P stoichiometry and nutrient limitation driven by
949 atmospheric nitrogen deposition. *Science*. 326:835-837.

950 Environment Canada. 2008. Canada-United States Air Quality Agreement Progress Report.
951 [http://www.ec.gc.ca/cleanair-airpur/caol/canus/report/2008CanUs /eng/tdm-
952 toc_eng.cfm](http://www.ec.gc.ca/cleanair-airpur/caol/canus/report/2008CanUs /eng/tdm-
952 toc_eng.cfm) (6/6/2009).

953 Epstein, H.E., Burke, I.C., Mosier, A.R. 2001. Plant effects on nitrogen retention in shortgrass
954 steppe 2 years after ¹⁵N addition. *Oecologia* 128:422-430.

955 Falkengren_Grerup, U. 1995. Interspecies differences in the preference of ammonium and nitrate
956 in vascular plants. *Oecologia* 102: 305-311.

957 Fenn, M.E., and Allen, E.B. In press. Southern Semi-Arid Highlands. In: Pardo, L.H., Robin-
958 Abbott, M.J., Driscoll, C.T., eds. Assessment of effects of N deposition and empirical
959 critical loads for nitrogen for ecoregions of the United States. USDA Forest Service
960 General Technical Report, xxx pp.

961 Fenn, M.E., Allen, E.B., Geiser, L.H. In press. Mediterranean California. In: Pardo, L.H., Robin-
962 Abbott, M.J., Driscoll, C.T., eds. Assessment of effects of N deposition and empirical
963 critical loads for nitrogen for ecoregions of the United States. USDA Forest Service
964 General Technical Report, xxx pp.

965 Fenn, M.E., Allen, E.B., Weiss, S.B., Jovan, S., Geiser, L., Tonnesen, G.S., Johnson, R.F., Rao,
966 L.E., Gimeno, B.S., Yuan, F., Meixner, T., Bytnerowicz, A. 2010. Nitrogen critical loads
967 and management alternatives for N-impacted ecosystems in California. *Journal of*
968 *Environmental Management* 91:2404-2423.

969 Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman,
970 W.D., Sickman, J.O., Meixner, T., Johnson, D.W., Neitlich, P. 2003a. Ecological effects of
971 nitrogen deposition in the western United States. *Bioscience*. 53(4): 404-420.

972 Fenn, M.E., de Bauer, L.I., Quevedo-Nolasco, A., Rodriguez-Frausto, C. 1999. Nitrogen and
973 sulfur deposition and forest nutrient status in the Valley of Mexico. *Water, Air, and Soil*
974 *Pollution* 113: 155-174.

975 Fenn, M.E., de Bauer, L.I., Zeller, K., Quevedo, A., Rodríguez, C. and Hernández-Tejeda, T.
976 2002c. Nitrogen and sulfur deposition in the Mexico City Air Basin: Impacts on forest
977 nutrient status and nitrate levels in drainage waters. In: Fenn, M.E., de Bauer, L.I.,
978 Hernández-Tejeda, T., eds. *Urban Air Pollution and Forests: Resources at Risk in the*

979 Mexico City Air Basin. Ecological Studies Series, Volume 156. New York, NY: Springer-
980 Verlag: 298-319.

981 Fenn, M.E., Geiser, L.H. In press. Temperate Sierra. In: Pardo, L.H., Robin-Abbott, M.J.,
982 Driscoll, C.T., eds. Assessment of effects of N deposition and empirical critical loads for
983 nitrogen for ecoregions of the United States. USDA Forest Service General Technical
984 Report, xxx pp.

985 Fenn, M.E., Haueber, R., Tonnensen, G.S., Baron, J.S., Grossman-Clarke, S., Hope, D., Jaffe,
986 D.A., Copeland, S., Geiser, L., Rueth, H.M., Sickman, J.O. 2003b. Nitrogen emission,
987 deposition, and monitoring in the Western United States. *Bioscience*. 53(4): 391-403.

988 Fenn, M.E., Jovan, S., Yuan, F., Geiser, L., Meixner, T., Gimeno, B.S. 2008. Empirical and
989 simulated critical loads for nitrogen deposition in California mixed conifer forests.
990 *Environmental Pollution*. 155: 492-511.

991 Fenn, M.E., and Poth, M.A. 1999. Temporal and spatial trends in streamwater nitrate
992 concentrations in the San Bernardino Mountains, southern California. *Journal of*
993 *Environmental Quality*. 28: 822-836.

994 FIA (Forest Inventory and Analysis). 2001. U.S. forest facts and historical trends. USDA Forest
995 Service FS-696. M

996 Fenn, M.E.; Poth, M.A.; Bytnerowicz, A.; Sickman, J.O.; Takemoto, B.K. 2003c. Effects of
997 ozone, nitrogen deposition, and other stressors on montane ecosystems in the Sierra
998 Nevada. In: Bytnerowicz, A.; Arbaugh, M.J.; Alonso, R. eds. *Developments in*
999 *Environmental Science*, volume 2: *Ozone Air Pollution in the Sierra Nevada: Distribution*
1000 *and Effects on Forests*. Amsterdam: Elsevier: 111-155.

1001 Galloway, J.N. 1998. The global nitrogen cycle: changes and consequences. *Environmental*
1002 *Pollution* 102:15-24.

1003 Galloway, J.N., Aber, J.D., Erisman, J.W., Seitzinger, S.P., Howarth, R.W., Cowling, E.B.,
1004 Cosby, B.J. 2003. The nitrogen cascade. *BioScience* 53:341-356.

1005 Geiser, L.H., Ingersoll, A.R., Bytnerowicz, A., Copeland, S.A. 2008. Evidence of enhanced
1006 atmospheric ammoniacal nitrogen in Hells Canyon NRA: Implications for natural and
1007 cultural resources. *Air and Waste Management Association*. 58: 1223-1234.

1008 Geiser, L.H., Jovan, S.E., Glavich, D.A., Porter, M. 2010. Lichen-based critical loads for
1009 nitrogen deposition in western Oregon and Washington Forests, USA. *Environmental*
1010 *Pollution*. 158:2412-2421.

1011 Geiser, L.H., and Nadelhoffer, K. In press. Taiga. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll,
1012 C.T., eds. Assessment of effects of N deposition and empirical critical loads for nitrogen
1013 for ecoregions of the United States. USDA Forest Service General Technical Report, xxx
1014 pp.

1015 Geiser, L.H., and Neitlich, P.N. 2007. Air pollution and climate gradients in western Oregon and
1016 Washington indicated by epiphytic macrolichens. *Environmental Pollution*. 145: 203-218.

1017 Gilliam, F.S. 2006. Response of the herbaceous layer of forest ecosystems to excess nitrogen
1018 deposition. *Journal of Ecology*. 94: 1176-1191.

1019 Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in forest ecosystems.
1020 *BioScience*. 57: 845-858.

1021 Gilliam, F.S., Adams, M.B., Yurish, B.M. 1996. Ecosystem nutrient responses to chronic
1022 nitrogen inputs at Fernow Experimental Forest, West Virginia. *Canadian Journal of Forest*
1023 *Research* 26:196-205.

1024 Gilliam, F.S., Goodale, C.L., Pardo, L.H., Geiser, L.H., Lilleskov, E.A. In press. Eastern
1025 temperate forest. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T., eds. Assessment of
1026 effects of N deposition and empirical critical loads for nitrogen for ecoregions of the
1027 United States. USDA Forest Service General Technical Report, xxx pp.

1028 Gilliam, F.S., Hockenberry, A.W., Adams, M.B. 2006. Effects of atmospheric nitrogen
1029 deposition on the herbaceous layer of a central Appalachian hardwood forest. *Journal of*
1030 *the Torrey Botanical Society*. 133: 240-254.

1031 Glavich, D.A., and Geiser, L.H. 2008. Potential approaches to developing lichen-based critical
1032 loads and levels for nitrogen, sulfur and metal-containing atmospheric pollutants in North
1033 America. *The Bryologist*. 111: 638–649.

1034 Gotelli, N.J., and Ellison, A.M. 2002. Nitrogen deposition and extinction risk in the northern
1035 pitcher plant, *Sarracenia purpurea*. *Ecology* 83:2758–2765.

1036 Gotelli, N.J., and Ellison, A.M. 2006. Forecasting extinction risk with nonstationary matrix
1037 models. *Ecological Applications* 16: 51-61.

1038 Greaver, T., Liu L., Bobbink R. In press. Wetlands. In: Pardo, L.H., Robin-Abbott, M.J.,
1039 Driscoll, C.T., eds. Assessment of effects of N deposition and empirical critical loads for
1040 nitrogen for ecoregions of the United States. USDA Forest Service General Technical
1041 Report, xxx pp.

1042 Grulke, N.E., Andersen, C.P., Fenn, M.E., and Miller, P.R. 1998. Ozone exposure and nitrogen
1043 deposition lowers root biomass of ponderosa pine in the San Bernardino Mountains,
1044 California. *Environmental Pollution*. 103: 63-73.

1045 Grulke, N.E., and Balduman, L. 1999. Deciduous conifers: High N deposition and O₃ exposure
1046 effects on growth and biomass allocation in ponderosa pine. *Water, Air and Soil Pollution*.
1047 116: 235-248.

1048 Grulke, N.E., Minnich, R.A., Paine, T.D., Seybold, S.J., Chavez, D.J., Fenn, M.E., Riggan, P.J.,
1049 Dunn, A. 2009. Air pollution increases forest susceptibility to wildfires: A case study in
1050 the San Bernardino Mountains in southern California. In: Bytnerowicz, A., Arbaugh, M.J.,
1051 Riebau, A.R., Andersen, C., eds. *Wildland Fires and Air Pollution. Developments in*
1052 *Environmental Science, Volume 8*. Amsterdam: Elsevier: 365-403.

1053 Hall, S.J. In press. Tropical and subtropical humid forests. In: Pardo, L.H., Robin-Abbott, M.J.,
1054 Driscoll, C.T., eds. *Assessment of effects of N deposition and empirical critical loads for*
1055 *nitrogen for ecoregions of the United States*. USDA Forest Service General Technical
1056 Report, xxx pp.

1057 Hettelingh, J-P., Posch, M., Slootweg, J. (eds.). 2008. *Critical Load, Dynamic Modelling and*
1058 *Impact Assessment in Europe*. CCE Status Report 2008, Coordination Centre for Effects.
1059 Netherlands Environmental Assessment Agency, www.pbl.nl/cce (www.mnp.nl/cce until
1060 [2009](http://www.pbl.nl/cce)).

1061 Hurd, T.M., Brach, A.R., Raynal, D.J. 1998. Response of understory vegetation of Adirondack
1062 forests to nitrogen additions. *Canadian Journal of Forest Research* 28: 799-807.

1063 Hyvärinen, M., Walter, B., Koopmann, R. 2003. Impact of fertilisation on phenol content and
1064 growth rate of *Cladonia stellaris*: a test of the carbon-nutrient balance hypothesis.
1065 *Oecologia*. 134:176-181.

1066 Inouye, R. S. 2006. Effects of shrub removal and nitrogen addition on soil moisture in sagebrush
1067 steppe. *Journal of Arid Environments*. 65: 604-618.

1068 Jones, M.E., Paine, T.D., Fenn, M.E., Poth, M.A. 2004. Influence of ozone and nitrogen
1069 deposition on bark beetle activity under drought conditions. *Forest Ecology and*
1070 *Management*. 200: 67-76.

1071 Jorgensen, E.E., Holub, S.M., Mayer, P.M., Gonsoulin, M.E., Silva, R.G., West, A.E., Tunnell,
1072 S.J., Clark, J.E., Parsons, J.L., Engle, D.M., Hellgren, E.C., Spears, J.D.H., Butler, C.E.,
1073 Leslie, D.M. Jr. 2005. Ecosystem stress from chronic exposure to low levels of nitrate.
1074 U.S. Environmental Protection Agency, National Risk Management Research Laboratory
1075 EPA/600/R-05/087. 35 pp.

1076 Jovan, S. 2008. Lichen bioindication of biodiversity, air quality, and climate: baseline results
1077 from monitoring in Washington, Oregon, and California. Gen. Tech. Rep. PNW-GTR-737.
1078 Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research
1079 Station. 56 pp.

1080 Jovan, S., and McCune, B. 2005. Air quality bioindication in the greater Central Valley of
1081 California with epiphytic macrolichen communities. *Ecological Applications*. 15(5): 1712-
1082 1726.

1083 Kelly, V.R., G.M. Lovett, K.C. Weathers, and G.E. Likens. 2005. Trends in atmospheric
1084 ammonium concentrations in relation to atmospheric sulfate and local agriculture.
1085 *Environmental Pollution* 135:363-369.

1086 Kleijn, D., Bekker, R.M., Bobbink, R., de Graaf, M.C.C., Roelofs, J.G.M. 2008. In search for
1087 key biogeochemical factors affecting plant species persistence in heathlands and acidic
1088 grasslands: a comparison of common and rare species. *Journal of Applied Ecology* 45:
1089 680-687.

- 1090 Knops, J.M.H, Nash, T.H. III, Boucher, V.L., Schlesinger, W.L. 1991. Mineral cycling and
1091 epiphytic lichens: implications at the ecosystem level. *Lichenologist*, 23: 309-321.
- 1092 Krupa, S.V. 2003. Effects of atmospheric ammonia (NH₃) on terrestrial vegetation: a review.
1093 *Environmental Pollution* 124:179-221.
- 1094 Kytöviita, M.-M., and Crittenden, P.D. 2007. Growth and nitrogen relations in the mat-forming
1095 lichens *Stereocaulon paschale* and *Cladonia stellaris*. *Annals of Botany* 100: 1537–1545.
- 1096 LeBauer, D. S. and Treseder, K. K. 2008. Nitrogen limitation of net primary productivity in
1097 terrestrial ecosystems is globally distributed. *Ecology*. 89(2): 371-379.
- 1098 Lafrancois, B.M., Nydick, K.R., Johnson, B.M., Baron, J.S. 2004. Cumulative effects of
1099 nutrients and pH on the plankton of two mountain lakes. *Canadian Journal of Fisheries and*
1100 *Aquatic Science*. 61: 1153-1165.
- 1101 Latimer J.S., and Rego, S.A. 2010. Empirical relationship between eelgrass extent and predicted
1102 watershed-derived nitrogen loading for shallow New England estuaries. *Estuarine, Coastal*
1103 *and Shelf Science*. 90:231-240.
- 1104 Lehmann, C.M.B., Bowersox, V.C., Larson, S.M. 2005. Spatial and temporal trends of
1105 precipitation chemistry in the United States, 1985-2002. *Environmental Pollution* 135:
1106 347-361.
- 1107 Lilleskov, E.A. 2005. How do composition, structure, and function of mycorrhizal fungal
1108 communities respond to nitrogen deposition and ozone exposure? In: Dighton, J., White,
1109 J.F., Oudemans, P., eds. *The Fungal Community: Its Organization and Role in the*
1110 *Ecosystem*. Boca Raton: Taylor & Francis.

- 1111 Lilleskov, E.A. 1999. Decline of above- and belowground ectomycorrhizal fungal diversity over
1112 an atmospheric nitrogen deposition gradient near Kenai, Alaska. Doctoral Dissertation,
1113 Cornell University, Ithaca.
- 1114 Lilleskov, E.A., Fahey, T.J., Horton, T.R., Lovett, G.M. 2002. Belowground ectomycorrhizal
1115 fungal community change over a nitrogen deposition gradient in Alaska. *Ecology* 83: 104-
1116 115.
- 1117 Lilleskov, E.A., Fahey, T.J., Lovett, G.M. 2001. Ectomycorrhizal fungal aboveground
1118 community change over an atmospheric nitrogen deposition gradient. *Ecological*
1119 *Applications* 11: 397-410.
- 1120 Lilleskov, E.A., Wargo, P.M., Vogt, K.A., Vogt, D.J. 2008. Mycorrhizal fungal community
1121 relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition
1122 gradient in the northeastern US. *Canadian Journal of Forest Research*. 38: 1260-1266.
- 1123 Liu L. and Greaver T.L. 2009. A review of nitrogen enrichment effects on three biogenic GHGs:
1124 The CO₂ sink may be largely offset by stimulated N₂O and CH₄ emission. *Ecology Letters*.
1125 12: 1103-1117.
- 1126 Lovett, G.M., T.Tear, D. Evers, S.E.G. Findlay, B.J. Cosby, J. Dunscomb, C. Driscoll and K.C.
1127 Weathers. 2009. Effects of air pollution on ecosystems and biological diversity in the
1128 eastern United States. *Annals of the New York Academy of Sciences*. 1162: 99-135.
- 1129 Makkonen, S., Hurri, R.S.K., Hyvarinen, M. 2007. Differential responses of lichen symbionts to
1130 enhanced nitrogen and phosphorus availability: An experiment with *Cladonia stellaris*.
1131 *Annals of Botany*. 99: 877-884.
- 1132 McCune, B., Dey, J., Peck, J., Heiman, K., Will-Wolf, S. 1997. Regional gradients in lichen
1133 communities of the southeast United States. *The Bryologist* 100: 145-158.

- 1134 McCune, B., Grenon, J., Mutch, L.S., Martin, E.P. 2007. Lichens in relation to management
1135 issues in the Sierra Nevada national parks. *Pacific Northwest Fungi*. 2: 1-39.
- 1136 McCune, B.M., Geiser, L.H. 2009. *Macrolichens of the Pacific Northwest*. 2nd Edition. Corvallis,
1137 OR: Oregon State University Press.
- 1138 McKane, R.B, Johnson, L.C., Shaver, G.R., Nadelhoffer, K.J., Rastetter, E.B., Fry, B., Giblin,
1139 A.E., Kielland, K., Kwiatkowski, B.L., Laundre, J.A., Murray, G. 2002. Resource-based
1140 niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*
1141 415: 68-71
- 1142 McNulty, S.G. and Boggs, J.L. 2010. A conceptual framework: redefining forest soil's critical
1143 acid loads under a changing climate. *Environmental Pollution* 158: 2053-2058.
- 1144 McNulty, S.G., Boggs, J., Aber, J.D., Rustad, L., Magill, A. 2005. Red spruce ecosystem level
1145 changes following 14 years of chronic N fertilization. *Forest Ecology and Management*
1146 219: 279-291.
- 1147 McNulty, S.G., Cohen, E.C., Myers, J.A.M., Sullivan, T.J., Li, H. 2007. Estimates of critical acid
1148 loads and exceedances for forest soils across the conterminous United States.
1149 *Environmental Pollution* 149: 281-292.
- 1150 Meixner, T., and Fenn, M. 2004. Biogeochemical budgets in a Mediterranean catchment with
1151 high rates of atmospheric N deposition—importance of scale and temporal asynchrony.
1152 *Biogeochemistry*. 70: 331-356.
- 1153 Michel, T.J., Saros, J.E., Interlandi, S.J., Wolfe, A.P. 2006. Resource requirements of four
1154 freshwater diatom taxa determined by in situ growth bioassays using natural populations
1155 from alpine lakes. *Hydrobiologia*. 568: 235-243.

1156 Miller, A.E., and Bowman, W.D. 2002. Variation in nitrogen-15 natural abundance and nitrogen
1157 uptake traits among co-occurring alpine species: do species partition nitrogen form?
1158 *Oecologia* 130:609-616

1159 Mitchell, R.J., Truscot, A.M., Leith, I.D., Cape, J.N., van Dijk, N., Tang, Y.S., Fowler, D.,
1160 Sutton, M.A. 2005. A study of epiphytic communities of Atlantic oak woods along an
1161 atmospheric nitrogen deposition gradient. *Journal of Ecology*. 93:482-492.

1162 Moore, T., Blodau, C., Turunen, J., Roulet, N., Richard, P.J.H. 2004. Patterns of nitrogen and
1163 sulfur accumulation and retention in ombrotrophic bogs, eastern Canada. *Global Change*
1164 *Biology* 11 (2): 256-367.

1165 Nadelhoffer, K., and Geiser, L.H. In press. Tundra. In: Pardo, L.H., Robin-Abbott, M.J.,
1166 Driscoll, C.T., eds. Assessment of effects of N deposition and empirical critical loads for
1167 nitrogen for ecoregions of the United States. USDA Forest Service General Technical
1168 Report, xxx pp.

1169 NADP. 2009. Atmospheric integrated research monitoring network. Available at
1170 <http://nadp.sws.uiuc.edu/airmon/>. Accessed May 17, 2010.

1171 NEG/ECP (New England Governors and Eastern Canadian Premiers) Forest Mapping Group.
1172 2003. Assessment of forest sensitivity to nitrogen and sulfur deposition in New England
1173 and Eastern Canada - pilot phase report. Boston: Conference of the New England
1174 Governors and Eastern Canadian Premiers. 16 p. Available at: [http://www.ecosystems-](http://www.ecosystems-research.com/fmi/reports/htm)
1175 [research.com/fmi/reports/htm](http://www.ecosystems-research.com/fmi/reports/htm).

1176 NRC (National Research Council). 2004. Air Quality Management in the United States. National
1177 Academy of Sciences Press, Washington, D.C., 462 pp.

1178 Nilles, M.A., and Conley, B.E. 2001. Changes in the chemistry of precipitation in the United
1179 States, 1981-1998. *Water, Air and Soil Pollution* 130: 409-414.

1180 Nordin, A., Strengbom, J., Ericson, L. 2006. Responses to ammonium and nitrate additions by
1181 boreal plants and their natural enemies. *Environmental Pollution* 141: 167-174.

1182 Nordin, A., Strengbom, J., Witzell, J., Näsholm, T., Ericson, L. 2005. Nitrogen deposition and
1183 the biodiversity of boreal forests: Implications for the nitrogen critical load. *Ambio*. 34:20-
1184 24.

1185 Nydick, K.R., Lafrancois, B.M., Baron, J.S., Johnson, B.M. 2004. Nitrogen regulation of algal
1186 biomass, productivity, and composition in shallow mountain lakes, Snowy Range,
1187 Wyoming, USA. *Canadian Journal of Fisheries and Aquatic Science*. 61: 1256-1268.

1188 Ollinger, S.V., Aber, J.D., Lovett, G.M. Milham, S.E., and Lathrop, R.G. 1993. A spatial model
1189 of atmospheric deposition for the northeastern US. *Ecological Applications*. 3: 459-472.

1190 Ouimet, R., Arp, P.A., Watmough, S.A., Aherne, J., Demerchant, I. 2006. Determination and
1191 mapping critical loads of acidity and exceedances for upland forest soils in eastern Canada.
1192 *Water, Air and Soil Pollution* 172: 57-66.

1193 Pardo, Linda H. 2010. Approaches for estimating Critical Loads of N and S Deposition for
1194 Forest Ecosystems on U.S. Federal Lands. Gen. Tech. Rep. NRS-71. Newtown Square,
1195 PA: U.S. Department of Agriculture, Forest Service, Northern Research Station 25 pp.

1196 Pardo, L.H., Geiser, L.H., Fenn, M, Driscoll, C.T, Goodale, C.L, Allen E, Baron, J. Bobbink, R.
1197 Bowman, W.D, Clark, C, Emmett, B, Gilliam, F.S, Greaver, T, Hall, S.J, Lilleskov, E.A,
1198 Liu, L, Lynch, J, Nadelhoffer, K, Perakis, S, Robin-Abbott, M.J, Stoddard, J, Weathers, K.
1199 In press b. Synthesis. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T., eds. Assessment

1200 of effects of N deposition and empirical critical loads for nitrogen for ecoregions of the
1201 United States. USDA Forest Service General Technical Report, xxx pp.

1202 Pardo, L.H., Goodale, C.L., Lilleskov, E.A., Geiser, L.H. In press c. Northern forest. In: Pardo,
1203 L.H., Robin-Abbott, M.J., Driscoll, C.T., eds. Assessment of effects of N deposition and
1204 empirical critical loads for nitrogen for ecoregions of the United States. USDA Forest
1205 Service General Technical Report, xxx pp.

1206 Pardo, L.H., Lilleskov, E.A., Geiser, L.H., Robin-Abbott, M.J. In press d. Methods. In: Pardo,
1207 L.H., Robin-Abbott, M.J., Driscoll, C.T., eds. Assessment of effects of N deposition and
1208 empirical critical loads for nitrogen for ecoregions of the United States. USDA Forest
1209 Service General Technical Report, xxx pp.

1210 Pardo, L.H., Robin-Abbott, M.J., Driscoll, C.T., In press e. Assessment of effects of N deposition
1211 and empirical critical loads for nitrogen for ecoregions of the United States. USDA Forest
1212 Service General Technical Report, xxx pp.

1213 Perakis, S., Geiser, L.H., Lilleskov, E.A. In press. Marine west coast forest. In: Pardo, L.H.,
1214 Robin-Abbott, M.J., Driscoll, C.T., eds. Assessment of effects of N deposition and
1215 empirical critical loads for nitrogen for ecoregions of the United States. USDA Forest
1216 Service General Technical Report, xxx pp.

1217 Poikolainen, J., Lippo, H., Hongisto, M., Kubin, E., Mikkola, K., Lindgren, M. 1998. On the
1218 abundance of epiphytic green algae in relation to the nitrogen concentrations of
1219 biomonitors and nitrogen deposition in Finland. *Environmental Pollution*. 102: 85-92.

1220 Porter, E., Blett, T., Potter, D., Huber, C. 2005. Protecting resources on federal lands:
1221 Implications of critical loads for atmospheric deposition of nitrogen and sulfur.
1222 *BioScience*. 55: 603-612.

- 1223 Posch, M., de Smet, P.A.M., Hettelingh, J.-P., Downing, R.J., eds. 1995. Calculation and
1224 mapping of critical thresholds in Europe. Status Report 1995. RIVM Rep. No. 259101004.
1225 Bilthoven, Netherlands: Coordination Center for Effects, National Institute for Public
1226 Health and the Environment. Available at: <http://www.mnp.nl/cce/publ/>.
- 1227 Posch, M., de Smet, P.A.M., Hettelingh, J.-P., Downing, R.J., eds. 2001. Modelling and mapping
1228 of critical thresholds in Europe. Status report 2001. RIVM Rep. No. 2591010xx. Bilthoven,
1229 The Netherlands: Coordination Center for Effects, National Institute for Public Health and
1230 the Environment. Available at: <http://www.mnp.nl/cce/publ/>.
- 1231 Pypker, T.G. 2004. Influence of canopy structure and epiphytes on the hydrology of Douglas-fir
1232 forests. Ph.D. Thesis. Oregon State University, Corvallis, Oregon.
- 1233 Rabalais, N.N. 2002. Nitrogen in aquatic systems. *Ambio* 31: 102–112.
- 1234 Rao, L.E. and E.B. Allen. 2010. Combined effects of precipitation and nitrogen deposition on
1235 native and invasive winter annual production in California deserts. *Oecologia* 62: 1035-
1236 1046.
- 1237 Rao, L.E., Allen, E.B., Meixner, T. 2010. Risk-based determination of critical nitrogen
1238 deposition loads for fire spread in southern California deserts. *Ecological Applications*.
1239 20:1320-1335.
- 1240 Rao, L. E., Parker, D.R., Bytnerowicz, A.: Allen, E.B. 2009. Nitrogen mineralization across an
1241 atmospheric nitrogen deposition gradient in southern California deserts. *Journal of Arid*
1242 *Environments* 73: 920-930.
- 1243 Robin-Abbott, M.J., and Pardo, L.H. In press. Ecosystem Classification. In: Pardo, L.H., Robin-
1244 Abbott, M.J., Driscoll, C.T., eds. Assessment of effects of N deposition and empirical

1245 critical loads for nitrogen for ecoregions of the United States. USDA Forest Service
1246 General Technical Report, xxx pp.

1247 Rochefort, L, Vitt,D.H., Bayley, S.E. 1990. Growth, production and decomposition dynamics of
1248 *Sphagnum* under natural and experimentally acidified conditions. Ecology. 71(5):1986-
1249 2000.

1250 Rueth, H.M., Baron, J.S. 2002. Differences in Englemann spruce forest biogeochemistry east and
1251 west of the Continental Divide in Colorado, USA. Ecosystems. 5: 45-57.

1252 Rueth, H.M., Baron, J.S., Allstott, E.J. 2003. Responses of Engelmann spruce forests to nitrogen
1253 fertilization in the Colorado Rocky Mountains. Ecological Applications 13: 664-673.

1254 Saros, J.E., Michel, T.J., Interlandi, S.J, Wolfe, A.P. 2005. Resource requirements of
1255 *Asterionella formosa* and *Fragilaria crotonensis* in oligotrophic alpine lakes: implications
1256 for recent phytoplankton community reorganizations. Canadian Journal of Fisheries and
1257 Aquatic Science. 62: 1681-1689.

1258 Schaberg, P.G., DeHayes, D.H., Hawley, G.J., Murakami, P.F., Strimbeck, G.R., McNulty, S.G.
1259 2002. Effects of chronic N fertilization on foliar membranes, cold tolerance, and carbon
1260 storage in montane red spruce. Canadian Journal of Forest Research 32: 1351-1359.

1261 Schwinning, S., Starr, B.I., Wojcik, N.J., Miller, M.E., Ehleringer, J.E., Sanford, R.L. 2005.
1262 Effects of nitrogen deposition on an arid grassland in the Colorado plateau cold desert.
1263 Rangeland Ecology and Management. 58: 565-574.

1264 Sickman, J.O., Melack, J.M., Stoddard, J.L. 2002. Regional analysis of inorganic nitrogen yield
1265 and retention in high-elevation ecosystems of the Sierra Nevada and Rocky Mountains.
1266 Biogeochemistry. 57: 341-374.

- 1267 Slootweg, J., Posch, M., Hettelingh, J.-P., eds. 2007. Critical loads of nitrogen and dynamic
1268 modelling: CCE Progress Report 2007. MNP Report 500090001. Coordination Centre for
1269 Effects, Bilthoven, The Netherlands.
- 1270 Stevens, C.J., Dise, N.B., Mountford, J.O., Gowing, D.J. 2004. Impact of nitrogen deposition on
1271 the species richness of grasslands. *Science* 303:1876-1879.
- 1272 Strengbom, J., Walheim, M., Näsholm, T., Ericson, L. 2003. Regional differences in the
1273 occurrence of understory species reflect nitrogen deposition in Swedish forests. *Ambio*.
1274 32:91-97.
- 1275 Sullivan, T.J., Cosby, B.J., Tonnessen, K.A., Clow, D.W. 2005. Surface water acidification
1276 responses and critical loads of sulfur and nitrogen deposition in Loch Vale watershed,
1277 Colorado. *Water Resources Research*. 41 W01021, doi:10.1029/2004WR003414, 2005.
- 1278 Suding, K.N., Gross, K.L., Houseman, G.R. 2004. Alternative states and positive feedbacks in
1279 restoration ecology. *Trends in Ecology & Evolution* 19:46-53.
- 1280 Sutton M., Reis, S., Baker, S.M.H., eds. 2009. Atmospheric Ammonia. Springer Science, 464 pp.
- 1281 Theodose, T.A., and Bowman, W.D. 1997. Nutrient availability, plant abundance, and species
1282 diversity in two alpine tundra communities. *Ecology*. 78: 1861-1872.
- 1283 Thomas, R.Q., Canham, C.D., Weathers, K.C., Goodale, C.L. 2010. Increased tree carbon
1284 storage in response to nitrogen deposition in the US. *Nature Geoscience* 3: 13-17.
- 1285 Tilman, D. 1987. Secondary succession and the pattern of plant dominance along experimental
1286 nitrogen gradients. *Ecological Monographs* 57:189-214.
- 1287 Tilman, D. 1993. Species richness of experimental productivity gradients: How important is
1288 colonization limitation. *Ecology* 74:2179-2191.

1289 Tonnesen, G., Wang, Z., Omary, M., Chien, C.J. 2007. Assessment of Nitrogen Deposition:
1290 Modeling and Habitat Assessment. California Energy Commission, PIER Energy-Related
1291 Environmental Research, CEC-500-2005-032.
1292 <http://www.energy.ca.gov/2006publications/CEC-500-2006-032/CEC-500-2006-032.PDF>
1293 UBA (UmweltBundesAmt). 2004. Manual on methodologies and criteria for mapping critical
1294 levels/loads and geographical areas where they are exceeded. Berlin: Federal
1295 Environmental Agency (UmweltBundesAmt). Available at <http://www.icpmapping.org>.
1296 U.S. Environmental Protection Agency. 1993. Air quality criteria for oxides of nitrogen. Rep.
1297 No. EPA/600/8-91/049aF-cF. Research Triangle Park, NC: Office of Health and
1298 Environmental Assessment, Environmental Criteria and Assessment Office; 3v. Available
1299 from: NTIS, Springfield, VA; PB95-124533, PB95-124525, and PB95-124517
1300 U.S. EPA (Environmental Protection Agency). 2007. Acid Rain and Related Programs: 2007
1301 Progress Report. <http://www.epa.gov/airmarkets/progree/docs/2007ARPRReport.pdf>.
1302 U.S. EPA (Environmental Protection Agency). 2008. *Integrated Science Assessment (ISA) for*
1303 *Oxides of Nitrogen and Sulfur—Ecological Criteria (Final Report)*. EPA/600/R- 08/082F.
1304 U.S. Environmental Protection Agency, National Center for Environmental Assessment—
1305 RTP Division, Office of Research and Development, Research Triangle Park, NC.
1306 Available at <http://cfpub.epa.gov/ncea/cfm/recordisplay.cfm?deid=201485>.
1307 USDA, NRCS, 2009. The PLANTS database (<http://plants.usda.gov>, 11 December 2009)
1308 National Plant Data Center, Baton Rouge, LA 70874-4490.
1309 Van den Berg, L.J.L, Dorland, E., Vergeer, Philippine, Hart, M.A.C., Bobbink, R., Roelofs,
1310 J.G.M. 2005. Decline of acid-sensitive plant species in heathland can be attributed to

1311 ammonium toxicity in combination with low pH. *New Phytologist* 166:551-564. Doi:
1312 10.1111/j.1469-8137.2005.01338.x.

1313 van Diepen, L.T.A. 2008. The role and diversity of arbuscular mycorrhizal fungi in *Acer*
1314 *saccharum* dominated forest ecosystems under natural and N-amended conditions.
1315 Doctoral dissertation, Houghton, Michigan: Michigan Technological University.

1316 van Diepen, L.T.A., Lilleskov, E.A., Pregitzer, K.S., Miller, R.M. 2007. Decline of arbuscular
1317 mycorrhizal fungi in northern hardwood forests exposed to chronic nitrogen additions.
1318 *New Phytologist* .176: 175-183.

1319 Vitt, D.H. 1994. An overview of factors that influence the development of Canadian peatlands.
1320 *Memoirs of the Entomological Society of Canada* 169: 7-20.

1321 Vitt, D.H., Wieder, K., Halsey, L.A., Turetsky, M. 2003. Response of *Sphagnum fuscum* to
1322 Nitrogen Deposition: A case study of ombrogenous peatlands in Alberta, Canada. *The*
1323 *Bryologist*. 1062: 235-245.

1324 Wallander, H. 1995. A new hypothesis to explain allocation of dry matter between mycorrhizal
1325 fungi and pine seedlings in relation to nutrient supply. *Plant and Soil* 169:243-248.

1326 Weathers, K, and Lynch, J.A. In press. Deposition. In: Pardo, L.H., Robin-Abbott, M.J., Driscoll,
1327 C.T., eds. Assessment of effects of N deposition and empirical critical loads for nitrogen
1328 for ecoregions of the United States. USDA Forest Service General Technical Report, xxx
1329 pp.

1330 Weathers, K.C., Simkin, S.M., Lovett, G.M., Lindberg, S.E. 2006. Empirical modeling of
1331 atmospheric deposition in mountainous landscapes. *Ecological Applications*. 16(4): 1590-
1332 1607.

- 1333 Wedin, D.A., and Tilman, D. 1996. Influence of nitrogen loading and species composition on the
1334 carbon balance of grasslands. *Science* 274:1720-1723.
- 1335 Weiss, S.B. 1999. Cars, cows, and checkerspot butterflies: Nitrogen deposition and management
1336 of nutrient-poor grasslands for a threatened species. *Conserv. Biol.* 13:1476-1486.
- 1337 Whytemare, A.B., Edmonds, R.L., Aber, J.D., Lajtha, K.. 1997. Influence of excess nitrogen
1338 deposition on a white spruce (*Picea glauca*) stand in southern Alaska. *Biogeochemistry* 38:
1339 173–187.
- 1340 Wigand, C., McKinney, R.A., Charpentier, M.A., Chintala, M.M., Thursby, G.B. 2003.
1341 Relationships of nitrogen loadings, residential development, and physical characteristics
1342 with plant structure in New England salt marshes. *Estuaries* 26: 1494-1504.
- 1343 Williams, M.W., and Tonnessen, K.A. 2000. Critical Loads for Inorganic Nitrogen Deposition in
1344 the Colorado Front Range, USA. *Ecological Applications* 10(6): 1648-1665.
- 1345 Wolfe, A.P., Baron, J.S., Cornett, R.J. 2001. Anthropogenic nitrogen deposition induces rapid
1346 ecological changes in alpine lakes of the Colorado Front Range (USA). *Journal of*
1347 *Paleolimnology.* 25: 1-7.
- 1348 Wolfe, A.P., Van Gorp, A.C., Baron, J.S. 2003. Recent ecological and biogeochemical changes
1349 in alpine lakes of Rocky Mountain National Park (Colorado, USA): a response to
1350 anthropogenic nitrogen deposition. *Geobiology.* 1: 153-168.
- 1351 Wu, W., and Driscoll, C.T. 2010. Impact of climate change on three-dimensional dynamic
1352 critical load functions. *Environmental Science and Technology* 44: 720-726.
- 1353 Yoshida, L.C., and Allen, E.B. 2004. ¹⁵N uptake by mycorrhizal *Artemisia californica* and the
1354 invasive *Bromus madritensis* of a N-eutrophied shrubland. *Biology and Fertility of Soil*
1355 39: 243-248.

Table 1 – Summary of critical loads of nutrient N for North American ecoregions

reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem Component	CL for N deposition <i>kg N ha⁻¹ yr⁻¹</i>	Reliability	Response	Comments	Study
Tundra	Prostrate dwarf shrubs	1-3	##	Changes in CO ₂ exchange, cover, foliar N, and community composition of vascular plants	N addition study, Greenland high arctic, P enhanced N effects.	Arens et al. 2008 ^a
Tundra	Lichens	1-3	(#)	Changes in lichen pigment production and ultrastructure, changes in lichen and bryophyte cover	N addition studies, high and low arctic, P enhanced or moderated N effects.	Arens et al. 2008 ^a , Hyvärinen et al. 2003 ^b , Makonen et al. 2007 ^b
Taiga	Forest	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 ,
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

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
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
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 Forest	Geiser et al 2010.
Northern Forests	Ectomycorrhizal fungi	5-7	#	Change in fungal community structure		Lilleskov et al. 2008
Northern Forests	Herbaceous cover species	>7 and <21	#	Loss of prominent species	Response observed in low-level fertilization experiment	Hurd et al. 1998
Northern Forests	Hardwood and Coniferous Forests	8	##	Increased surface water NO ₃ ⁻ leaching		Aber et al. 2003
Northern Forests	Old-growth montane red spruce	>10 and <26	#	Decreased growth and/or induced mortality	Response observed in low-level fertilization experiment	McNulty et al. 2005

Northern Forests	Arbuscular mycorrhizal fungi	<12	(#)	biomass decline and community composition change		van Diepen 2008, van Diepen et al. 2007
Northwest Forested Mountains	Alpine lakes	1.5	##	Diatom assemblages	As wet deposition only	Baron 2006
Northwest Forested Mountains	Lichens	1.2-3.7	(#)	Epiphytic lichen community change in mixed-conifer forests, Alaska	Application of western Oregon and Washington model	Geiser et al. 2010
Northwest Forested Mountains	Lichens	2.5-7.1	##	Epiphytic lichen community change, thallus N enrichment in mixed-conifer forests, non-Alaska		Fenn et al. 2008, Geiser et al. 2010
Northwest Forested Mountains	Sub-alpine forest	4	##	Increase in organic horizon N, foliar N, potential net N mineralization, and soil solution N, initial increases in N leaching below the organic layer		Rueth and Baron 2002, Baron et al. 1994
Northwest Forested Mountains	Alpine lakes	4.0	#	Episodic freshwater acidification		Williams and Tonnesson 2000
Northwest Forested Mountains	Alpine grassland	4-10	##	Plant species composition		Bowman et al. 2006
Northwest 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

Northwest Forested Mountains	Mixed conifer forest	17	##	NO ₃ ⁻ leaching, reduced fine root biomass		Fenn et al. 2008
Marine West Coast Forest	Western OR and WA forests	2.7-9.2	##	Epiphytic lichen community change	Loss of oligotrophic species, enhancement of eutrophic species. CL increases with regional range in mean annual precipitation from 45-450 cm	Geiser et al. 2010
Marine West Coast Forest	SE Alaska forests	5	(#)	Fungal community change; declines in ectomycorrhizal fungal diversity		Lilleskov 1999; Lilleskov et al. 2001, 2002 ; Whytemare et al. 1997
Eastern Temperate Forest	Eastern Hardwood Forest	>3	#	Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood		Thomas et al. 2010
Eastern Temperate Forest	Lichens	4-8	(#)	Epiphytic lichen community change	Loss of oligotrophic species. Synergistic/confounding effects of acidic deposition not considered; based on application of model and estimated response threshold	Geiser et al. 2010
Eastern Temperate Forest	Southeast Coastal Plain	5-10	(#)	Ectomycorrhizal fungi community response		Dighton et al. 2004; Lilleskov et al. 2001, 2002, 2008

Eastern Temperate Forest	Eastern Hardwood Forests	8	##	Increased surface water loading of NO ₃ ⁻		Aber et al. 2003
Eastern Temperate Forest	Michigan deposition gradient	<12	(#)	Arbuscular mycorrhizal fungal biomass decline and community composition change		van Diepen 2008, van Diepen et al. 2007
Eastern Temperate Forest	Herbaceous species	<17.5	(#)	Increases in nitrophilic species, declines in species-rich genera (e.g., <i>Viola</i>)		Gilliam 2006, 2007; Gilliam et al. 2006
Great Plains	Tall-grass 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
Great Plains	Mixed-grass prairie	10-25	#	Soil NO ₃ ⁻ pools, leaching, plant community shifts		Clark et al. 2003, 2005; Jorgenson et al. 2005
Great Plains	Short-grass prairie	10-25	(#)		Inferred from mixed grass	Epstein 2001, Barret and Burke 2002
Great Plains	Mycorrhizal fungi	12	(#)	Decline in arbuscular mycorrhizal fungal activity		Egerton-Warburton
North American Desert	lichens	3	(#)	Lichen community shifts, thallus N concentration	Uncertainty regarding modeled estimates	Geiser et al. 2008, Porter et al. 2007
North American Desert	shrubland, woodland, desert grassland	3-8.4	#	Vegetation response, vascular plant community change		Allen et al. 2009; Baez et al. 2007; Inouye 2006; Rao et al. 2009, 2010

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.	Fenn et al. in press, Egerton-Warburton and Allen 2000, Tonnesen et al. 2007
Mediterranean California	Chaparral; Lichens	3-6	#	Epiphytic lichen community change	Lichen critical load is from modeled N deposition data and published data for lichens.	Geiser et al. 2010; Jovan 2008; Jovan and McCune 2005;
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, b, c; Fenn and Poth 1999; Meixner and Fenn 2004
Mediterranean California	Mixed conifer forest; Lichens	3.1-5.2	##	Lichen chemistry and community changes	The lowest critical load is based on lichen tissue chemistry above the clean site threshold.	Fenn et al. 2008
Mediterranean California	Mixed conifer forest; plant physiology	17	#	Reduced fine root biomass		Fenn et al. 2008; Grulke et al. 1998
Mediterranean California	Mixed conifer forest; soil processes	17-25.9	#	NO ₃ ⁻ leaching; soil acidification		Breiner et al. 2007, Fenn et al. 2008

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
Mediterranean California	Serpentine grassland	6	##	Annual grass invasion, replacing native herbs	Critical load based on a local roadside gradient; Serpentine grassland site is actually west of the Central Valley.	Weiss 1999; Fenn et al. 2010
Temperate Sierras	Lichens	4-7	(#)	Epiphytic lichen community change	Increase in proportion of eutrophic species. Estimated from MWCF model, response threshold allows ~60% eutrophs due to dry, hot climate, hardwood influence	Geiser et al. 2010
Temperate Sierras	Las Cruces and Chichinautzin Ranges S/SW of Mexico City	15	#	Elevated NO ₃ ⁻ in stream and spring waters	Data are from <i>Pinus hartwegii</i> sites in the Desierto de los Leones National Park and Ajusco	Fenn et al. 1999, 2002
Tropical and Subtropical humid forests	N-rich forests	<5-10	(#)	NO ₃ ⁻ leaching, N trace gas emissions	CL for N-rich forests should be lower than for N-poor forests based on possibility of N losses.	ND
Tropical and Subtropical Humid Forests	N-poor forests	5-10	(#)	Changes in community composition; NO ₃ ⁻ leaching, N trace gas emissions	CL for N-poor forests based on estimates for Southeastern Coastal Plain forests.	ND

Wetlands	Freshwater wetlands	2.7-13	#	Peat accumulation and NPP	CL for a wetlands in the northeastern U.S. and southeastern Canada	Aldous 2002 ^c , Moore et al. 2004 ^c , Rochefort and Vitt 1990 ^c , Vitt et al 2003 ^c
Wetlands	Freshwater wetlands	6.8-14	(#)	Pitcher plant community change	CL based on northeastern populations	Gotelli and Ellison 2002, 2006
Wetlands	Intertidal wetlands	50-100	##	Loss of eelgrass		Latimer and Rego 2010
Wetlands	Intertidal salt marshes	63-400	(#)	Salt marsh community structure, microbial activity and biogeochemistry		Caffrey et al. 2007, Wigand et al. 2003
Aquatic	Western Lakes	2	##	Freshwater eutrophication		Baron 2006
Aquatic	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

Table 2 – Assessment and interpretation of empirical critical loads of nutrient N for North American ecoregions

Ecoregion	Factors affecting the range of CL ^a	Comparison within Ecoregion ^b
Tundra	<ol style="list-style-type: none"> 1) moisture 2) competition between vascular plants and cryptogams 3) P-limitation 4) temperature 5) pH 	<p>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.</p>
Taiga	<ol style="list-style-type: none"> 1) soil depth 2) vegetation type and species composition 3) latitude 	<p>Morphological damage to lichens has been observed at a lower deposition in forests and woodlands than in shrublands or bogs and fens; cryptogam dominated mats on thin soils become N saturated faster than forest islands.</p>
Northern Forest	<ol style="list-style-type: none"> 1) receptor 2) tree species 3) stand age 4) site history 5) pre-existing N status 	<p>CLs for lichen are generally lowest, followed by CLs for ectomycorrhizal fungi and NO₃⁻ leaching. CLs for herbaceous species and forests are generally higher than for other responses.</p>
Northwest Forested Mountains	<ol style="list-style-type: none"> 1) biotic receptor 2) accumulated load of N 3) ecosystem 4) region 	<p>In alpine regions, diatom changes in lakes are seen at lowest the CL. Changes in individual plants are seen next, followed by vegetation community change, then soil responses. In subalpine forests, the CL of 4 kg ha⁻¹ yr⁻¹ for foliar and soil chemistry changes is similar to the lichen CL of 3.1 – 5.2 for lichen community change.</p>
Marine West Coast Forest	<ol style="list-style-type: none"> 1) background N status 2) soil type 3) species composition 4) fire history 5) climate 	<p>The midrange of responses reported for lichens (2.7 – 9.2 kg ha⁻¹ yr⁻¹) is broadly comparable to that for plant, soil, and mycorrhizal responses (5 kg ha⁻¹ yr⁻¹), despite limited studies for non-lichen responses.</p>

Eastern Forests	<ol style="list-style-type: none"> 1) precipitation 2) soil cation fertility and weathering 3) biotic receptors 	The CL for NO_3^- leaching, lichen community change, and ectomycorrhizal fungal response are within the same range. Arbuscular mycorrhizal fungal and herbaceous CLs are higher.
Great Plains	<ol style="list-style-type: none"> 1) N status 2) receptor 3) precipitation 	CLs are lower in the tall grass prairie than in the mixed- and short-grass prairies. CL in tall- and mixed-grass prairie is lower on N poor sites and sites with very N responsive plant species. CL in the short-grass prairie is likely lower in wet years than in dry years.
North American Deserts	<ol style="list-style-type: none"> 1) receptor 2) interaction of annual grasses with native forb cover 2) precipitation 	The lichen CL is lowest, at $3 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; vegetation CL varies from $3\text{-}20 \text{ kg N ha}^{-1} \text{ yr}^{-1}$
Mediterranean California	<ol style="list-style-type: none"> 1) Presence of invasive exotic annual grasses interacting with a highly diverse native forb community 2) N-sensitivity of mycorrhizal fungi 3) N-sensitivity of lichens 4) N retention capacity of catchments, catchment size 5) co-occurrence of ozone and ozone-sensitive tree species. 	The lowest CLs in Mediterranean California are for sensitive lichen in chaparral and oak woodlands and mixed conifer forests. The CL for plant and mycorrhizal fungal community change in coastal sage scrub is higher, at $7.8 \text{ to } 10 \text{ kg ha}^{-1} \text{ yr}^{-1}$. CL for NO_3^- leaching is lower in chaparral and oak woodlands ($10 \text{ -} 14 \text{ kg ha}^{-1} \text{ yr}^{-1}$) than in mixed conifer forests ($17 \text{ kg ha}^{-1} \text{ yr}^{-1}$). CLs are highest for mixed conifer forest plant community change and sustainability.
Wetlands	<ol style="list-style-type: none"> 1) vegetation species 2) the fraction of rainfall in the total water budget 3) the degree of openness of N cycling 	CL is much higher for intertidal wetlands ($50\text{-}400 \text{ kg ha}^{-1} \text{ y}^{-1}$) than for freshwater wetlands ($2.7\text{-}14 \text{ kg ha}^{-1} \text{ y}^{-1}$), which have relatively close water and N cycles.

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

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

Table 3 – Empirical critical loads of nutrient N for mycorrhizal fungi in U.S. ecoregions

reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem (Site)	CL for N deposition <i>kg ha⁻¹ yr⁻¹</i>	Reliability	Response of	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 morphotype 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
Northwest 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	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 unquantified. CL estimated from regression	Lilleskov 1999, Lilleskov et al. 2001, 2002, Whytemare et al. 1997
Eastern Temperate Forests	Southeast 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	Pine Barrens (New Jersey;	<8	(#)	Ectomycorrhizal fungal morphotype	Bulk deposition. Gradient study	Dighton et al. 2004

Ecoregion	Ecosystem (Site)	CL for N deposition <i>kg ha⁻¹ yr⁻¹</i>	Reliability	Response of	Comments	Study
Forests	Southeast Coastal Plain)			community change	with three sample points	
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	CL estimated from logarithmic curve of soil N vs. AMF activity. No low N baseline, so CL may be lower.	Egerton-Warburton
Mediterranean California	Coastal sage scrub (southern California)	7.8-9.2	#	Arbuscular mycorrhizal fungi, decrease in % colonization, spore density, spore richness	CL estimated from logarithmic curve fitted to data from this study compared to modeled and inferential N deposition data	Egerton-Warburton and Allen 2000, Tonnesen et al. 2007

1 **Table 4 – Empirical critical loads of nutrient N for lichens in U.S. ecoregions**
 2 ## reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem (Site)	CL for N deposition <i>kg ha⁻¹ yr⁻¹</i>	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	CL proposed based on values in the Taiga and Northwest Forested Mountains.	Geiser et al. 2010
Northwest Forested Mountains	Coniferous forests, Alaska	1.2-3.7	(#)	Lichen community composition	Application of western Oregon and Washington model	Geiser et al. 2010
Northwest Forested Mountains	Coniferous Forests, non- Alaska	2.5-7.1	##	Lichen community composition	Application of western Oregon and Washington model	Geiser et al. 2010
Northwest Forested Mountains	Central Southern Sierras	3.1-5.2	##	Shifts in epiphytic lichen communities favoring eutrophs	CL based on exceedance of a N concentration threshold in the	Fenn et al. 2008

Ecoregion	Ecosystem (Site)	CL for N deposition <i>kg ha⁻¹ yr⁻¹</i>	Reliability	Response of	Comments	Study
Marine West Coast Forests	Western OR and WA forests	2.7-9.2	##	Shifts in epiphytic lichen communities favoring eutrophs	lichen <i>Letharia vulpina</i> CL 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		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.	CL estimated from overlay of course grid (36 km) CMAQ N; local N deposition from NH ₃ was likely higher.	Geiser et al. 2008, Porter et al. 2007
Mediterranean California	Oak woodlands and chaparral (Central Valley: Sacramento Valley, Coast Ranges and Sierra foothills)	3-6	#	Shifts in epiphytic lichen communities favoring eutrophs	FHM lichen survey of 118 forested sites. Eutrophs dominated communities when CMAQ 4 km N dep estimates were >5.5 kg ha ⁻¹ yr ⁻¹	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
Temperate Sierras	Lichens	4-7	(#)	Shifts in epiphytic lichen communities favoring eutrophs	Increase in proportion of eutrophic species.	Geiser et al. 2010

3 a– based on data from Greenland; b – based on data from Finland; c – based on data from Canada; d –
4 based on data from Sweden
5

6 **Table 5 – Empirical critical loads of nutrient N for herbaceous plants and shrubs**
 7 **in U.S. ecoregions**

8 ## reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem (Site)	CL for N $kg\ ha^{-1}\ yr^{-1}$	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	Tall-grass 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	Short-grass prairie	10-25	(#)		Inferred from mixed grass.	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, Rao et al. 2009, 2010

Ecoregion	Ecosystem (Site)	CL for N <i>kg ha⁻¹ yr⁻¹</i>	Reliability	Response	Comments	Study
Mediterranean California	Serpentine grassland	6	##	Annual grass invasion, replacing native herbs	Critical load based on a local roadside gradient; Serpentine grassland site is actually west of the Central Valley.	Weiss 1999; Fenn et al. 2010
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.	Fenn et al. in press, Egerton-Warburton et al. 2001, 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, unpublished data ; Fenn et al. 2008
Wetlands	Freshwater wetlands	6.8-14	(#)	Pitcher plant community change	CL based on northeastern populations	Gotelli and Ellison 2002, 2006
Wetlands	Intertidal wetlands	50-100	##	Loss of eelgrass		Latimer and Rego 2010
Wetlands	Intertidal salt marsh	63-400	(#)	Salt marsh community structure, microbial activity and biogeochemistry		Caffrey et al. 2007, Wigand et al. 2003

9 a - based on data from Greenland; b – based on data from Sweden
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Table 6 – Empirical critical loads of nutrient N for forest ecosystems in U.S. ecoregions

reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem (Site)	CL for N $kg\ ha^{-1}\ yr^{-1}$	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	sub-alpine 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		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 nutritional 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

Ecoregion	Ecosystem (Site)	CL for N <i>kg ha⁻¹ yr⁻¹</i>	Reliability	Response	Comments	Study
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
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.	Fenn et al. 2008; Grulke et al., 1998
Mediterranean California	Mixed conifer forests (San Bernardino mountains)	25.9	#	Soil acidification; pH <= 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.	Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004 N deposition data from Fenn et al. 2008.
Tropical and Subtropical Humid Forests	N-poor tropical and subtropical forests	5-10	(#)	ND	CL for N-poor forests based on estimates for Southeastern Coastal Plain forests.	ND
Tropical and Subtropical Humid Forests	N-rich tropical and subtropical forests	<5-10	(#)	ND	CL for N-rich forests should be lower than for N-poor forests based on possibility of N losses.	ND

16
17
18

19 **Figure legends**

20 **Figure 1-- Ecological Regions of North America, Level I**

21 From the Commission for Environmental Cooperation (1997)

22

23 **Figure 2 -- Estimates of wet + dry nitrogen (N) deposition** in $\text{kg ha}^{-1} \text{ yr}^{-1}$ (includes wet

24 ammonium and nitrate, dry nitric acid, particulate nitrate and ammonium, and gaseous ammonia,

25 but not organic forms) generated by the CMAQ 2001 model for the more than 3200 locations for

26 which we report ecological responses to N deposition.

27

28 **Figure 3 – Map of (a) critical loads and (b) exceedances for mycorrhizal fungi by ecoregion**

29 **in the United States**

30 The range of critical loads reported for mycorrhizal fungi is shown for each ecoregion. The hatch

31 marks indicate increasing level of uncertainty: no hatch marks for the most certain "reliable"

32 category, single hatching for the "fairly reliable" category, and double hatching for the "expert

33 judgment" category. The color sequence moves from red toward blue and violet as the critical

34 load increases. As the range of the critical load gets broader, the saturation of the color

35 decreases.

36 Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance

37 (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within

38 +/-1 of the CL range, (3) Above CL_{\min} , when deposition is above the lower end of the CL range,

39 but lower than the upper end of the range, (4) Above CL_{\max} , when deposition is above the upper

40 end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able

41 to calculate exceedance for Alaska.

42

43 **Figure 4 - Map of (a) critical loads and (b) exceedances for lichens by ecoregion in the**
44 **United States**

45 The range of critical loads reported for lichens is shown for each ecoregion. The hatch marks
46 indicate increasing level of uncertainty: no hatch marks for the most certain "reliable" category,
47 single hatching for the "fairly reliable" category, and double hatching for the "expert judgment"
48 category. The color sequence moves from red toward blue and violet as the critical load
49 increases. As the range of the critical load gets broader, the saturation of the color decreases.

50

51 Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance
52 (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within
53 +/-1 of the CL range, (3) Above CL_{min} , when deposition is above the lower end of the CL range,
54 but lower than the upper end of the range, (4) Above CL_{max} , when deposition is above the upper
55 end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able
56 to calculate exceedance for Alaska.

57

58 **Figure 5 – Map of (a) critical loads and (b) exceedances for herbaceous plants and shrubs**
59 **by ecoregion in the United States.**

60 The range of critical loads reported for herbaceous plants and shrubs is shown for each
61 ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most
62 certain "reliable" category, single hatching for the "fairly reliable" category, and double hatching
63 for the "expert judgment" category. The color sequence moves from red toward blue and violet

64 as the critical load increases. As the range of the critical load gets broader, the saturation of the
65 color decreases.

66 Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance
67 (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within
68 +/-1 of the CL range, (3) Above CL_{min} , when deposition is above the lower end of the CL range,
69 but lower than the upper end of the range, (4) Above CL_{max} , when deposition is above the upper
70 end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able
71 to calculate exceedance for Alaska.

72

73 **Figure 6 – Map of (a) critical loads and (b) exceedances for forest ecosystems by ecoregion**
74 **in the United States.**

75 The range of critical loads reported for forest ecosystems is shown for each ecoregion; this map
76 does not include the responses of mycorrhizal fungi, lichens, or understory herbaceous plants
77 already represented. The hatch marks indicate increasing level of uncertainty: no hatch marks for
78 the most certain "reliable" category, single hatching for the "fairly reliable" category, and double
79 hatching for the "expert judgment" category. The color sequence moves from red toward blue
80 and violet as the critical load increases. As the range of the critical load gets broader, the
81 saturation of the color decreases.

82 Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance
83 (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within
84 +/-1 of the CL range, (3) Above CL_{min} , when deposition is above the lower end of the CL range,
85 but lower than the upper end of the range, (4) Above CL_{max} , when deposition is above the upper

86 end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able
87 to calculate exceedance for Alaska.

88

89 **Figure 7 – Map of (a) critical loads and (b) exceedances based on increased nitrate leaching**
90 **by ecoregion in the United States.**

91 The range of critical loads based on increased nitrate leaching for each ecoregion. The hatch
92 marks indicate increasing level of uncertainty: no hatch marks for the most certain "reliable"
93 category, single hatching for the "fairly reliable" category, and double hatching for the "expert
94 judgment" category. The color sequence moves from red toward blue and violet as the critical
95 load increases. As the range of the critical load gets broader, the saturation of the color
96 decreases.

97 Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance
98 (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within
99 +/-1 of the CL range, (3) Above CL_{min} , when deposition is above the lower end of the CL range,
100 but lower than the upper end of the range, (4) Above CL_{max} , when deposition is above the upper
101 end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able
102 to calculate exceedance for Alaska.

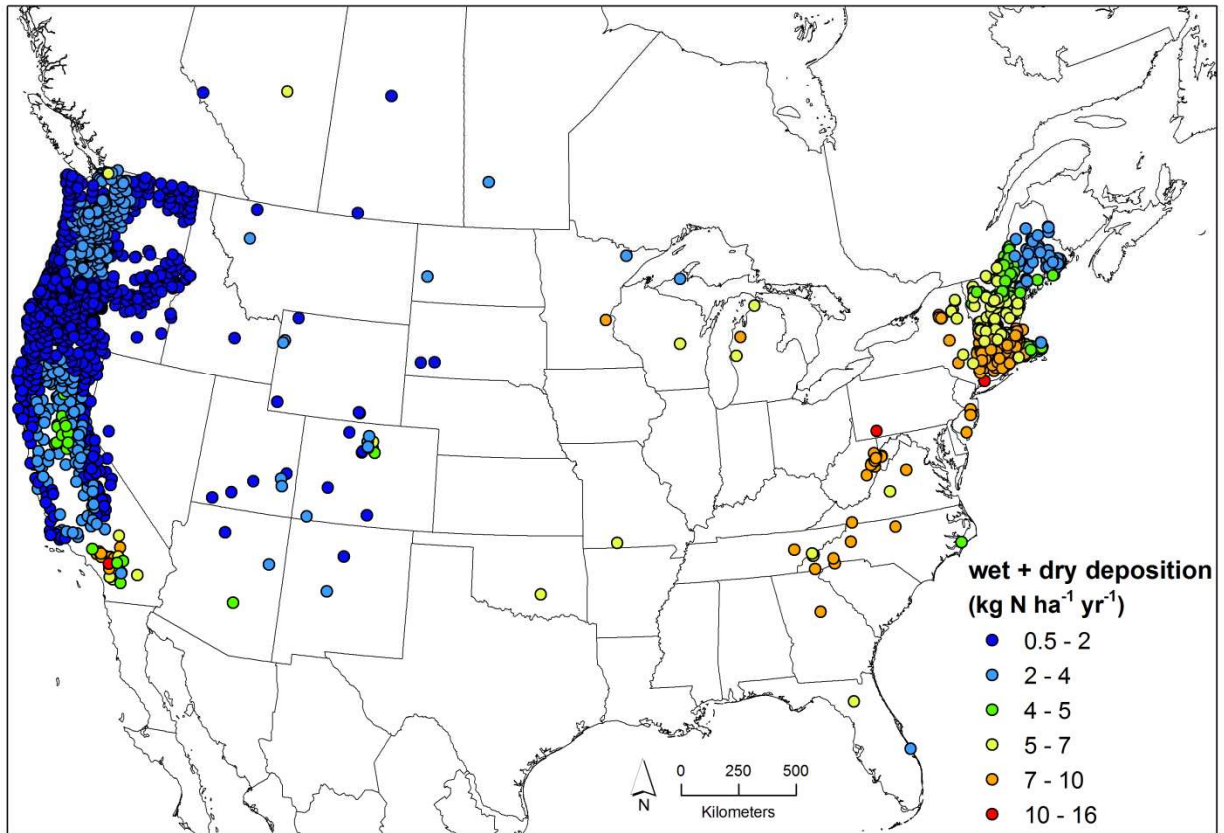
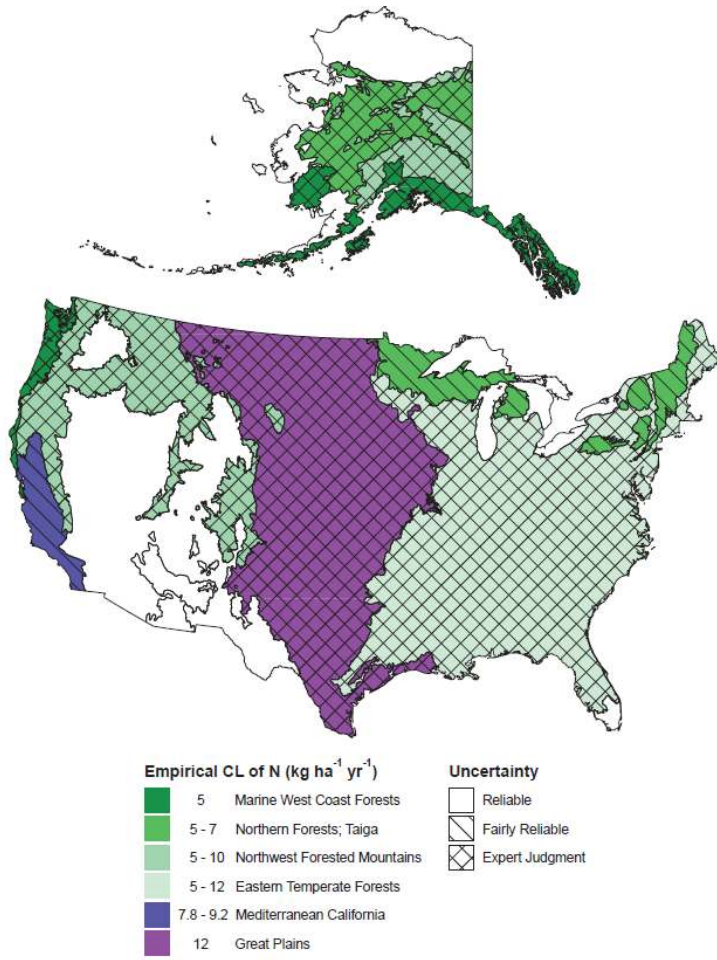


Figure 1

a.



b.

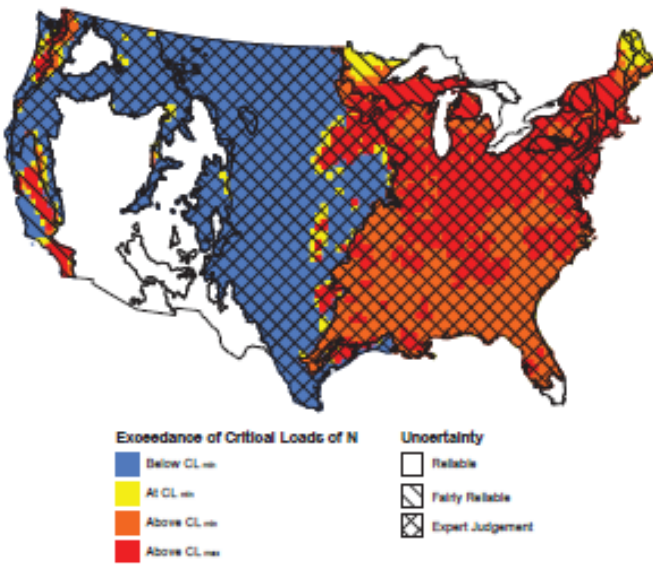
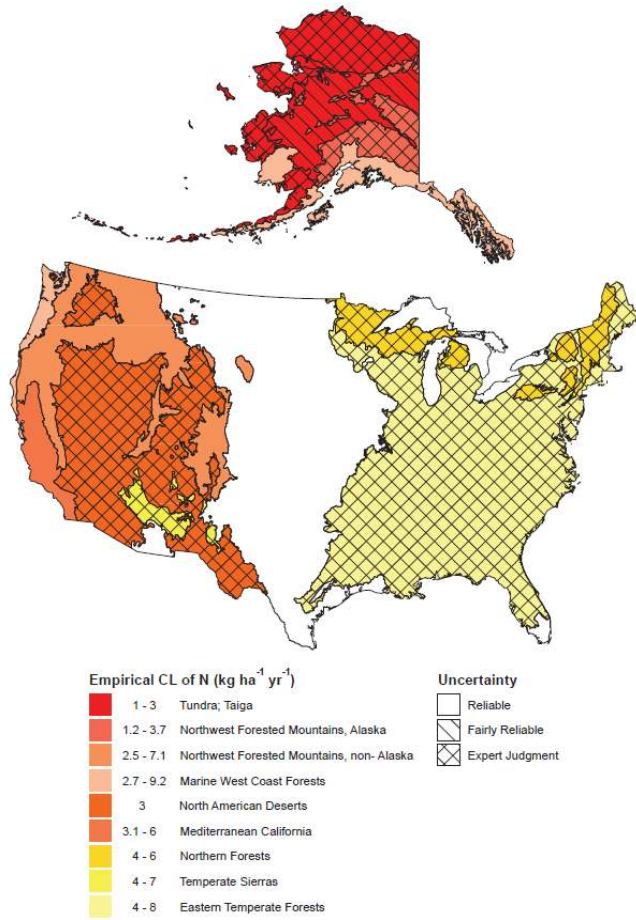


Figure 2

a.



b.

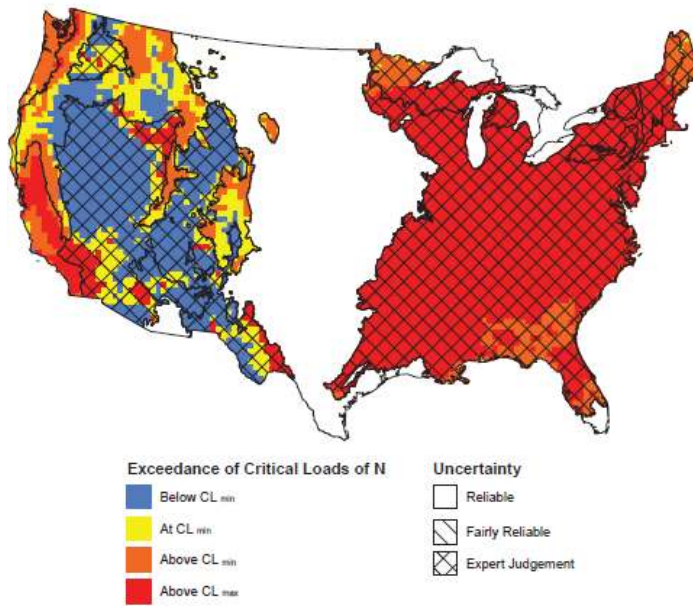
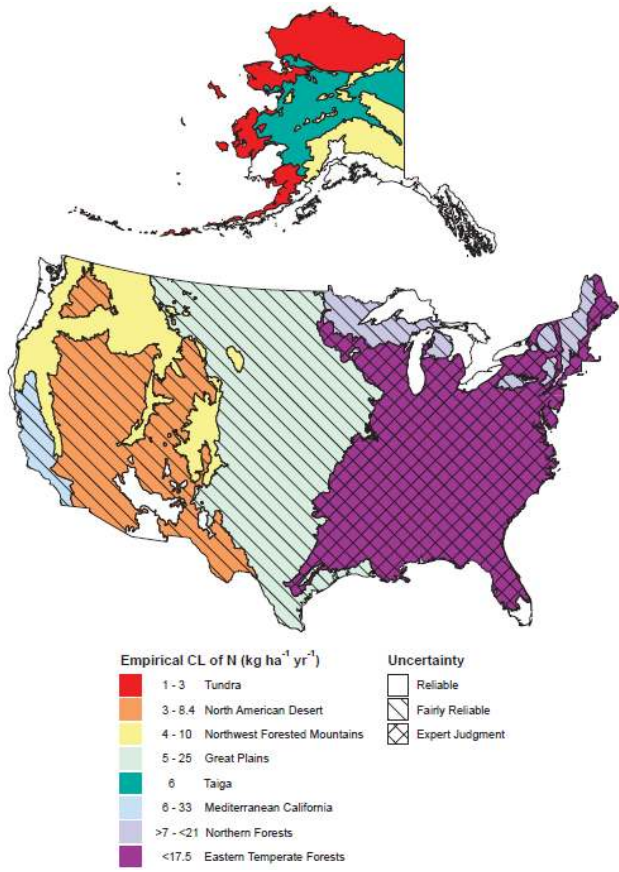


Figure 3

a.



b.

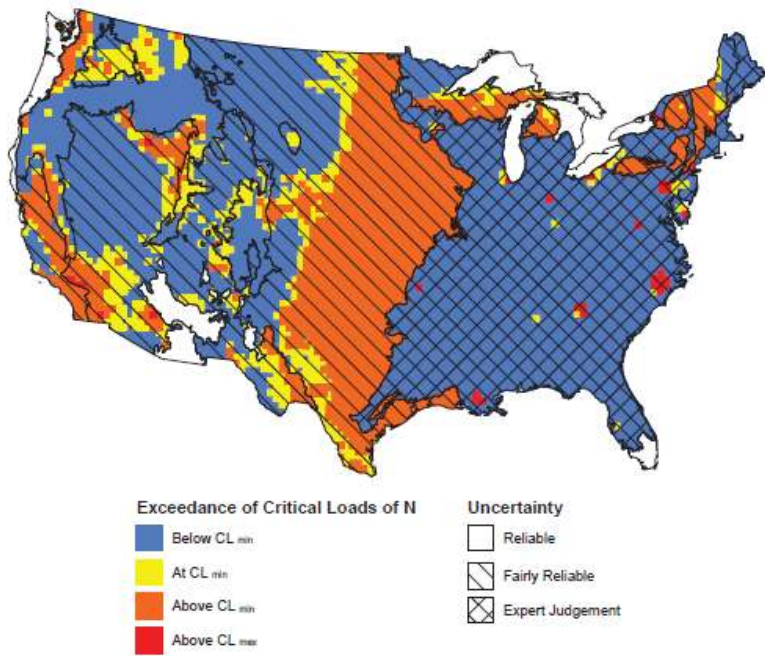
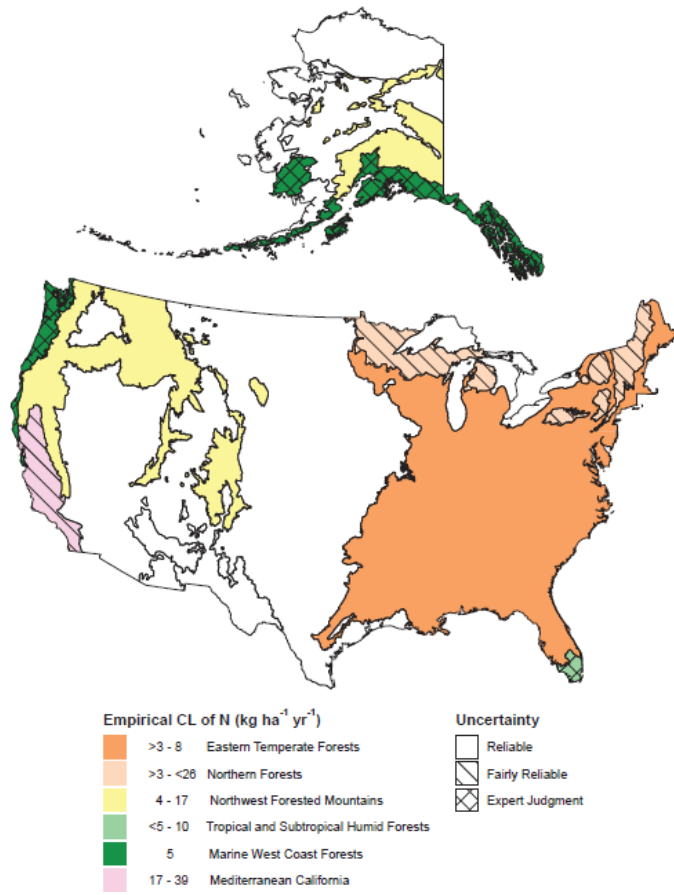


Figure 4

a.



b.

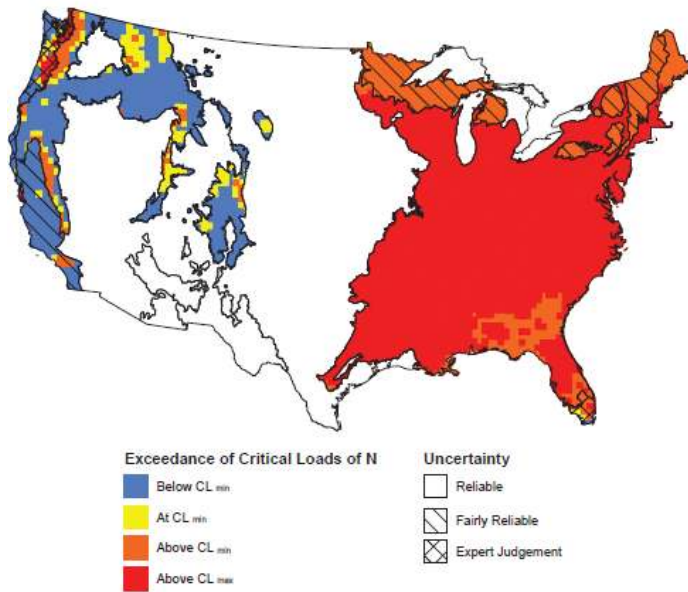
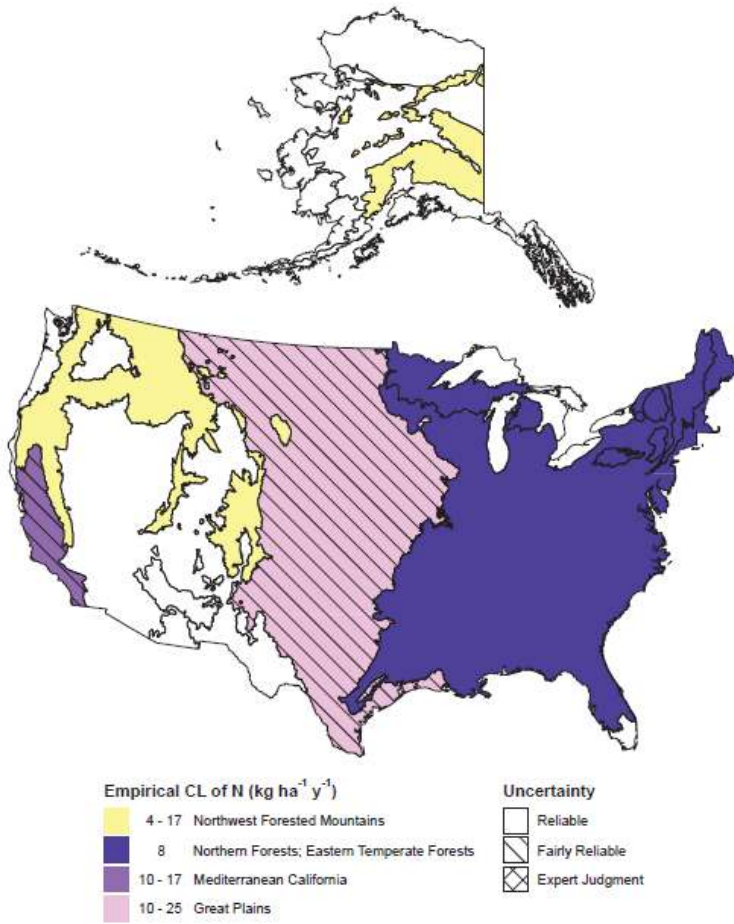


Figure 5

a.



b.

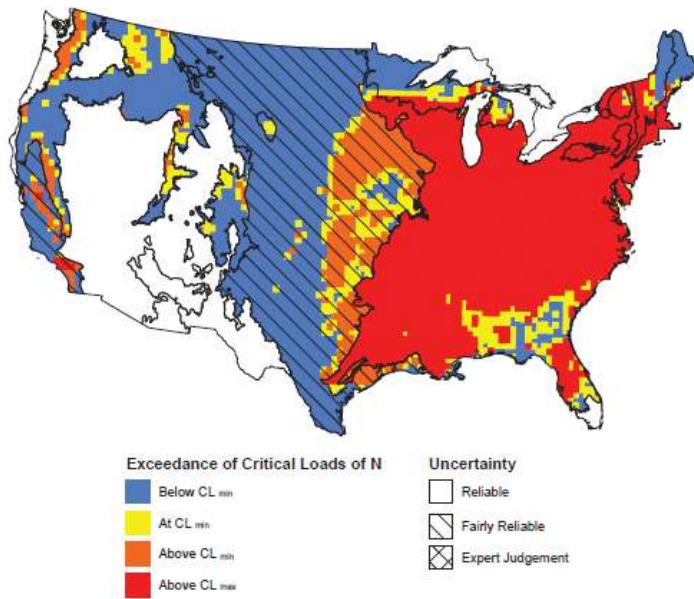


Figure 6