6 TAIGA

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6.1 Ecoregion Description

The Taiga ecoregion (CEC 1997; Figure 2.1) includes most of interior Alaska and much of Canada's northern boreal forest. The ecoregion description is adapted from CEC (1997). The Alaskan portion is underlain by horizontal limestone, shale, and sandstones, creating a flat to gently rolling plain covered with organic deposits, hummocky moraines, and lacustrine deposits; the eastern portion is underlain by the Canadian Shield. Lowlands are mostly peatlands and permafrost is widespread. Nutrient-poor soils dominate southern portions and permafrost soils occur in the north. The climate is subarctic: the short summers have long daylight and cool temperatures; winters are long and very cold. Snow and freshwater ice persist for 6 to 8 months annually. Mean annual temperatures are -10 to 0 °C; mean annual precipitation is 200 to 500 mm. Innumerable lakes, bogs, other wetlands, and forests are interspersed with tundra-like shrublands and sedge meadows. In the north, forests transition to woodlands with a lichen groundcover and finally merge into tundra at the climatic limits of tree growth. Mid-zone, dwarf birch (*Betula nana*), Labrador tea (*Ledum* spp.), willow (*Salix* spp.), bearberry (*Arctostaphylos alpina*), mosses, and sedges dominate. In the south, open stands of stunted black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) are accompanied by alder (*Alnus* spp.), willow, and tamarack (*Larix larcinia*) in fens and bogs. White spruce (*Picea glauca),*black spruce, lodgepole pine (*Pinus contorta*), quaking aspen (*Populus tremuloides*), balsam polar (*Populus balsamifera*), and paper birch (*Betula papyrifera*) grow on well drained, warm upland sites, rivers, and streams. Mat-forming lichens can constitute in excess of 60 percent of the winter food intake of caribou and reindeer (Longton 1997). The abundant wetlands attract hundreds of thousands of birds (e.g., ducks, geese, loons, and swans) which come to nest, or rest and feed on their way to arctic breeding grounds.

6.2 Ecosystem Responses

Responses to increased nitrogen (N) deposition in boreal regions (which include Taiga and Northern Forests ecoregions) include increased productivity, foliar N concentration, and N leaching from soils, plant community changes (including vascular plants, bryophytes, lichens, and algae), and physiological changes. In boreal ecosystems and other largely oligotrophic environments, N is growth-limiting, and most plant species are adapted to low available N. As N availability increases, faster growing, but less N-use efficient species (more N taken up per unit growth) typically outcompete slower growing species (Aerts and Chapin 2000). Increasing N deposition alters plant community structure, often leading to a short-term "positive" response of increased productivity and vigor, followed by long-term changes in species composition and richness (Gough et al. 2000). Such community-level responses occur at low deposition rates and have been used to mark the low end of ecosystem N response (Bobbink et al. 2003, de Vries et al. 2007). In boreal forests, overall ground flora species number may not be affected by N enrichment, despite a drastic change in species composition, due to reciprocal increases in nitrophilous species with declines in typical species (Bobbink 2004). However, in peatland bogs, where high water levels and low pH prevent nitrophyte invasions (Allen 2004), decline in species richness is a more characteristic response.

Increased N supply is often accompanied by increased foliar N concentration, which in turn may increase susceptibility of vegetation to frost or diseases. This effect is documented for boreal forest trees (e.g., Aronsson 1980, Balsberg-Påhlsson 1992, Kallio et al. 1985, Schaberg et al. 2002), for their common understory ericaceous species (e.g., Strengbom et al. 2002, 2003), and for bogs (e.g., Wiedermann et al. 2007). At higher deposition levels, as N is no longer completely taken up by vegetation or immobilized in soils, N saturation and leaching may occur (Lamontagne 1998; Lamontagne and Schiff 1999, 2000; Tamm et al. 1999).

The severity of N deposition impacts depends on: duration and amount of N deposition, the form(s) of atmospheric N, the sensitivity of the ecosystem components; other environmental conditions; and management history (Bobbink et al. 2003). As a result, ecosystem response to N loading varies temporally, spatially, and by habitat type. Change or loss of habitats can have direct implications on the animals using these habitats.

6.3 Range of Responses Observed

Like the Tundra ecoregion, the paucity of North American studies and the many similarities in climate, topography, and vegetation communities across the circumboreal environment support consideration of European findings to predict ecosystem N responses for North America. Therefore, we include European data in this discussion of the range of observed responses. European analyses considered Taiga and Northern Forest ecoregions (CEC 1997) as a single boreal biogeographic region under the European University Information System (EUNIS) classification system; hence the frequent use of the term 'boreal' in the following sections. Responses to N inputs are summarized in Table 6.1.

6.3.1 Deposition

Our knowledge of current N deposition and deposition effects in the North American taiga is limited. Wet deposition of inorganic N at the National Atmospheric Deposition Program (NADP) monitors at Denali National Park and Preserve and Fairbanks, Alaska, has been low and stable, averaging 0.23 kg ha^{-1} yr^{-1} (std. dev. = 0.129) from 1981 to 2007 (NADP 2008). Total nitrate (NO_3^-) deposition in snow at two interior Alaska sites north of Fairbanks in 1988 was consistent with this range and averaged 0.32 kg N ha^{-1} (Jaffe and Zukowski 1993). Recent measurements of N from ammonium (NH_4^+) and NO_3^- ions in throughfall deposition at remote sites in northeastern Alberta, Canada (Berryman and Straker 2008) ranged from 0.6 to 2.0 kg N ha^{-1} yr^{-1}.

6.3.2 Forests and Woodlands

Plant community composition changes. A large number of studies, summarized by Bobbink et al. (2003), have demonstrated increases in abundance of nitrophilous species with increased N deposition over time and along N gradients. In Swedish boreal forests, changes in ground vegetation, e.g., decreasing whortleberry (*Vaccinium myrtillus*), occurred at deposition rates ≥ 6 kg N ha^{-1} yr^{-1} (Nordin et al. 2005, Strengbom et al. 2003) and increased growth of wavy hairgrass (*Deschampsia flexuosa*) at ≥ 5 kg N ha^{-1} yr^{-1} (Kellner and Redbo-Torstensson 1995, Nordin et al. 2005).

In an N fertilization experiment with 0, 12.5, and 50 kg N ha^{-1} yr^{-1} (background atmospheric deposition 2 to 3 kg N ha^{-1} yr^{-1}), the abundance of wavy hairgrass increased significantly after 3 years with 12.5 kg N ha^{-1} yr^{-1} while the abundance of whortleberry decreased (Strengbom et al. 2002). Bryophyte species are also responsive; the biomass of Schreber's big red stem moss (*Pleurozium schreberi*) and a dicranum moss (*Dicranum polysetum*) fertilized with 25 and 30 kg N ha^{-1} yr^{-1} was reduced by 60 percent and 78 percent, respectively, after 4 years (Mäkipää 1998).

Pest and disease resistance. In a large-scale field study of 557 coniferous stands in Sweden, the occurrences of whortleberry, lingonberry (V*accinium vitis-idaea)* and wavy hairgrass, were investigated (Strengbom et al. 2003). Where N deposition was ≥ 6 kg ha^{-1} yr^{-1}, whortleberry was less frequent and more susceptible to the fungal leaf pathogen *Valdensia heterodoxa*. Frequency of lingonberry was also strongly negatively correlated with increasing N deposition (Strengbom et al. 2003).

Whortleberry showed increased parasite burdens at N fertilization ≥ 12.5 kg ha^{-1} yr^{-1} (Nordin et al. 1998, 2005; Strengbom et al. 2002). Disease incidence by the fungus *Valdensia heterodoxa* was more than twice as high in plots receiving 12.5 kg N ha^{-1} yr^{-1} and more than three times as high in plots receiving 50 kg N ha^{-1} yr^{-1} compared to controls. The abundance of the fungus *V. heterodoxa* on whortleberry was increased tenfold by 25 kg N ha^{-1} yr^{-1} compared to 0.5 kg N ha^{-1} yr^{-1}. As a consequence, whortleberry density decreased, and wavy hairgrass cover increased (Strengbom et al. 2002). In addition, shoots of whortleberry were significantly more damaged by moth larvae such as the rusty tussock moth (*Orgyia antique*) after addition of 12.5 kg N ha^{-1} yr^{-1} in the first year of treatment (Nordin et al. 1998). Cover of wavy hairgrass continued to increase over 5 years of N additions between 8 and 12 kg ha^{-1} yr^{-1}, induced by increased light penetration resulting from disease damage to whortleberry (Nordin et al. 2005).

Cold tolerance. Frost hardiness and plant tissue cold hardiness can be reduced by N additions. For example, after 12 years of fertilization with ammonium chloride (NH_4Cl) at 15 kg N ha^{-1} yr^{-1}, first-year foliage in red spruce (*Picea rubens*) at a high elevation forest in New England (with ambient wet + dry deposition of ~10 kg N ha^{-1} yr^{-1}) showed diminished cold tolerance, greater electrolyte leakage, and increased susceptibility to frost damage (Schaberg et al. 2002). Nutrient imbalances created by N and sulfur (S) fertilization and low potassium (K), phosphorus (P), and magnesium (Mg) status in southern Sweden and Denmark have been shown to increase the risk for development of cold temperature-related bark lesions in beech (*Fagus* spp.); advance bud burst of needles, putting young needles at risk for frost damage by a temperature backlash; and increase the frost-sensitivity of the inner bark and needles of Norway spruce (*Picea abies*) (Jönsson et al. 2000, 2001, 2004a, 2004b).

N storage in cryptogam mats. Woodlands or tree-islands of pine with ground vegetation of mat-forming lichens are a common taiga vegetation type. In general, when inorganic N is received in low concentrations, either from natural rainfall (Hyvärinen and Crittenden 1998b) or applied in solution (Crittenden 1998), the estimated uptake efficiency of (non-N_2-fixing) mat-forming lichens has ranged from 90 to 100 percent. Internal recycling of N and P in mat-forming lichens improves nutrient-use efficiency and is likely ecologically important in N- and P-limited environments typical of the taiga (Crittenden et al. 1994, Kytöviita and Crittenden 2007). Much of the eastern portion of the Taiga ecoregion is underlain by the Canadian Shield and soils can be shallow and acidic. During a short-term experimental addition of 40 kg N ha^{-1} yr^{-1} to a small catchment of boreal pine-reindeer lichen (*Pinus-Cladonia*) forest in Ontario, Canada, the higher export of mineral N from lichen-dominated bedrock surfaces compared to treed soil islands was attributed to the lower retention of N deposition in combination with leaching of mineralized N from lichen and moss patches (Lamontagne 1998). Net nitrification increased or remained similar to reference sites in lichen patches, while N-amended forest islands had a strong tendency to consume NO_3^- and produce NH_4^+ (Lamontagne and Schiff 2000). By the second year, lichen-covered bedrock surfaces no longer retained N additions. In contrast, N-amended and reference forest islands retained a similar proportion of N inputs, indicating that forest islands did not become N saturated in this time frame. However, because the components of the boreal shield landscape are hydrologically connected, there is concern that long-term N deposition to such a heterogeneous landscape will ultimately lead to N saturation of habitats with relatively high N retention capacities (Lamontagne and Schiff 1999). Finally, organic forms of N (e.g., free amino acids) serve as important plant N sources, and N deposition can disrupt the ratio between organic and mineral N supply in boreal soils (Näsholm et al. 1998, Nordin et al. 2001).

Epiphytic lichens and algae. Jack pine and black spruce boreal forests of northeastern Alberta were sampled at 5, 10, 15, 20, 25, 30, 50, 60, 80, 100, and 120 km along cardinal directions from the Athabasca Oil Sands operations, a major source of nitrogen oxide (NO_x) and sulfur dioxide (SO_2) emissions for Canada. Nitrogen and S in the mat-forming gray-green reindeer lichen (*Cladina rangiferina*) and in two epiphytes, a tube (*Hypogymnia physodes*) and ring (*Evernia mesomorpha*) lichen, decreased with distance and were elevated within 30 km of the operations. Lichen community composition was weakly correlated with distance: sensitive shrubby beard and horsehair lichens were less abundant and showed dwarfing, hyper-growth of asexual structures, discoloration of the lichen, and increased parasitism by fungi at sites close to the Athabasca Oil Sands (Berryman et al. 2004). Preliminary data indicate that N deposition in canopy throughfall under jack pine forests at clean sites ranges from 0.6 to 2.0 kg ha^{-1} yr^{-1}, increasing to 3.0 kg ha^{-1} yr^{-1} at sites near the mines. A new study is under way to relate deposition measures and modeled estimates of N and S to lichen response and to elucidate the relative roles of SO_2, NO_x, metals, and alkaline dust from mining operations in observed community responses (Berryman and Straker 2008). The correlation of N accumulated by lichen thalli with measures of deposition or distance from a point source is consistent with other studies in boreal forests in Eurasia (Bruteig 1993, Crittenden 2000, Crittenden et al. 1994, Hyvärinen and Crittenden 1998a, Walker et al. 2003). Information on lichen research methodology and terminology can be found in Chapter 4 of this report.

During a 10-year monitoring period in Sweden, patterns for sensitive epiphytic lichens were opposite to those observed for algae (Bråkenhielm and Quinghong 1995). The number of individuals, total cover, and proportion of sensitive lichens decreased with growing season length and with increasing N and S deposition; the first marked decrease occurred as N deposition exceeded 5 to 8 kg N ha^{-1} yr^{-1}. In contrast, colonization rate and colony thickness of epiphytic green algae (mainly *Protococcus viridis*) increased with increases in deposition and growing season length, especially as N deposition exceeded 12 kg ha^{-1} yr^{-1}. Poikolainen et al. (1998) observed increases in the abundance of green algae on conifers at lower deposition levels than did the Swedish researchers. Based on observations from 3009 permanent Finnish forest plots between 1985 and 1995, increased algal cover was associated with N deposition levels as low as 3 kg ha^{-1} yr^{-1}. Nitrogen concentration in the epiphytic tube lichen, *Hypogymnia physodes*, the splendid feather moss (*Hylocomium splendens*), Schreber's big red stem moss, and bark of Scots pine (*Pinus sylvestris*) were also correlated with N deposition. Temperature was confounded with N and S deposition in both studies, as both temperature and deposition decrease in more northerly latitudes.

Additions of N can cause changes in physiology and ultrastructure in common lichens of taiga ecosystems. In an electron microscopy study of the epiphytic horsehair (*Bryoria capillaris*) and tube (*Hypogymnia physodes*) lichens, treatments of 560 µg m^{-3} nitrogen dioxide (NO_2) or 10 mM sodium nitrate ($NaNO_3$), ammonium chloride (NH_4Cl), and ammonium nitrate (NH_4NO_3) induced accumulation of electron-opaque substances in the vacuoles of both the algal and fungal cells and general degeneration of the fungal cells (Holopainen and Karenlampi 1985). This demonstrates that N additions can influence cellular structure and metabolic processes in lichens—an important functional group in both boreal and arctic regions. See Chapter 5 (Tundra) for descriptions of effects on mat-forming and other terricolous lichens.

Ectomycorrhizal fungi. There is no information on ectomycorrhizal community responses to N in the Taiga ecoregion. We postulate that, given the climate, species composition and soils, white and black spruce dominated ecosystems may have similar deposition thresholds to those seen in spruce forests of the same species in coastal Alaska (see Chapter 9, West Coast Marine Forests) and to those of the spruce-fir forests of the northeastern United States (see Chapter 7, Northern Forests).

6.3.3 Ericaceous Shrublands (Heaths)

Heathlands are dwarf shrub communities that form on shallow peat or drained soils. Nitrogen-enrichment responses of heathland plant communities are characterized by increased growth of grasses and decreased growth of dwarf shrubs, lichens, and bryophytes (Allen 2004). Initially, shrubs respond to N additions with increased growth and tissue N concentrations, and the first adverse effects are shade-induced declines in lichen and bryophyte cover (Cornelissen et al. 2001). However, long-term N enrichment decreases root biomass and increases the susceptibility of shrubs to insect attack and frost. These effects, together with increased competition from grasses, cause a deterioration of the dominant shrub community. During a 5-year fertilization study (10.8 kg ha^{-1} yr^{-1} modeled ambient total deposition plus a 10 kg N ha^{-1} yr^{-1} application) of low-alpine heather (*Calluna vulgaris*) heaths in the Cairngorm Mountains of Scotland, species richness was reduced by exposure to added N deposition (Britton and Fisher 2007). The lichen component of the vegetation was most sensitive to N additions, although vascular plants were also affected via interactions with climate (Britton and Fisher 2007). Curtis et al. (2005) used isotope tracers in other European heaths and moorlands to demonstrate that bryophytes and lichens were important sinks for N deposition, reducing the amount of inorganic N available to both higher plants and soil microbes in grassland and ericoid shrub-dominated catchments. However, as N deposition increased from 2 to 30 kg ha^{-1} yr^{-1}, these sinks became saturated and cryptogam biomass decline was accompanied by increased NO_3^- leaching (see also Emmett 2007).

6.3.4 Peatlands

Peatlands are moss-dominated bogs and fens that are prevalent in the Taiga ecoregion. About 43 percent of Alaska can be classified as wetlands, much of that peatlands, contrasting strongly with the contiguous 48 states where wetlands comprise barely 5 percent of the total land area (Hall et al. 1994). The sensitivity of peatlands to N deposition decreases along a poor-to-rich productivity gradient from ombrotrophic bogs, which receive nearly all nutrient inputs from the atmosphere, to poor and rich fens, which receive additional nutrients from slow moving ground water and mineral sources (Vitt et al. 2003). The general progression of N deposition effects is:

1) At 0.7 to 8.1 kg N ha^{-1} yr^{-1} peat accumulation increases with N deposition due to increases in net photosynthesis and growth of previously N-limited mosses (Moore et al. 2004, Vitt et al. 2003). With average bulk deposition of 0.81 kg N ha^{-1} yr^{-1} and 1.14 kg S ha^{-1} yr^{-1} from 2005 to 2008, a dominant sphagnum moss (*Sphagnum fuscum)* in 10 remote bogs across northeastern Alberta was N-limited, and no differences in moss growth or net primary productivity were observed compared to previously published values for this area (Wieder et al. 2010).There are some indications that net photosynthesis in this sphagnum species may peak as early as 3 kg N ha^{-1} yr^{-1} in some Canadian peatlands (Vitt et al. 2003). (Oligotrophic mosses are the predominant N-sink and biomass in peatlands).
2) At 12 to 18 kg N ha^{-1} yr^{-1}, growth rates do not increase further and mosses begin to accumulate foliar N (Lamers et al. 2000, Moore et al. 2004, Vitt et al. 2003).
3) At >18 kg N ha^{-1} yr^{-1}, the natural moss N filter fails and N begins to leach from the saturated moss layer, altering competitive relationships (Lamers et al. 2000). Vegetation changes are characterized by decreases in cover of oligotrophic mosses and carnivorous plants and increases in graminoids, especially cotton grass and certain ericaceous shrubs (Allen 2004).

Chapter 17 (Wetlands) contains a more detailed discussion of these and interrelated responses, especially in relation to P availability, water availability, and climate.

6.3.5 Tundra

Areas of tundra are included in the Taiga ecoregion, notably at the northern boundaries. See Chapter 5 (Tundra) for descriptions of the range of responses.

6.4 Critical Loads Estimates

There are many indications that low levels of N deposition can affect community composition, abundance, net photosynthesis, N accumulation, physiology, and ultrastructure of lichens, mosses, and algae (see Table 6.1). These taxa, especially peatland sphagnum mosses and reindeer lichens, are dominant components of taiga ecosystems. Application here of a model relating epiphytic lichen community composition of Oregon and Washington coniferous forests to N deposition (Chapter 4, Geiser et al. 2010) yields a critical load estimate of 1 to 3 kg ha^{-1} yr^{-1} for Taiga ecoregion forests and woodlands. This value was calculated by substituting a realistic precipitation range of 20 to 80 cm and applying a conservative community-composition response threshold allowing no less than 41 percent oligotrophs or more than 27 percent eutrophs. For perspective, about 85 percent of sites in the western Oregon and Washington study area did not exceed this response threshold (Geiser et al. 2010). Considering this result and those of Moore et al. (2004), Vitt et al. (2003), Strengbom et al. (2003), Berryman et al. (2004), Berryman and Straker (2008), and Poikolainen et al. (1998), we recommend that the critical load for lichen, moss, and algae of the North American Taiga ecoregion be no more than 1 to 3 kg ha^{-1} yr^{-1}. This estimate can be considered fairly reliable, pending results from more definitive work currently in progress in North America. Critical loads are summarized in Table 6.2.

Table 6.1—Responses to N input relevant to the North American taiga. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	Critical load for N dep. *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Epiphytic lichens	1-3	(#)	Community composition shift	Application of model developed for Marine West Coast Forests ecoregion to the Taiga ecoregion	Geiser et al. 2010, Chapter 4
Peatlands, NE Canada	2.7-8.1	#	Increase in peat accumulation	N addition and gradient studies	Moore et al. 2004
Boreal forest, Sweden	<3	(#)	Decreased frequency of the shrub lingonberry, especially in spruce (as opposed to pine) stands	Possible interactions with other biotic and abiotic factors	Strengbom et al. 2003
Black spruce and jack pine forests, NE Alberta	3	(#)	Increased lichen N concentrations, morphological damage to and decreased abundance of sensitive epiphytic lichens	N effects likely confounded and/or amplified by elevated SO_2, alkaline dust and/or metal deposition	Berryman et al. 2004; Berryman and Straker 2008
Boreal forest, Finland	3	(#)	Increased cover of green algae on conifers	Increasing temperature, decreasing S may also be contributing to increased algal cover	Poikolainen et al. 1998
Peatlands, NE Alberta	>3	#	Gradual decrease in net primary photosynthesis of *Sphagnum fuscum*	Combined multiple N- addition studies	Vitt et al. 2003
Boreal forest, Sweden	5-8	(#)	Decreases in the proportion of N-sensitive epiphytic lichens	Confounding temperature effect	Bråkenhielm and Quinghong 1995
Boreal forest, Sweden	6	##	Increase in grass cover, esp. wavy hairgrass; decreased growth of shrubs whortleberry and lingonberry	Long term experiment in area with low background deposition using low N addition rates	Nordin et al. 2005
Boreal forest, Sweden	6	#	Decreased frequency of the shrub, whortleberry, concurrent with rates of parasitism by *Valdensia heterodoxa*	Possible interactions with other biotic and abiotic factors	Strengbom et al. 2003
Low-alpine heather heaths, Cairngorm Mtns, Scotland	5-15	#	Reduced species richness of lichens; also higher plants via interactions with climate		Britton and Fisher 2007
Northern Europe	10-15; 10-20	#	Increased mineralization, nitrification and N leaching of soils		Bobbink et al. 2003, de Vries et al. 2007

Northern Europe	10-15	#	Changes in composition and cover of understory vascular plants, bryophytes, lichens, and free-living algae		Bobbink et al. 2003, de Vries et al. 2007
Northern Europe	10-20	(#)	Reduced sporocarp production, changed/reduced below-ground mycorrhizal species composition		Bobbink 2003, de Vries et al. 2007
Boreal forest, Sweden	<12	#	Increased fungal parasitism of whortleberry by *Valdensia heterodoxa*; enhanced growth of wavy hairgrass from defoliation of parasitized whortleberry and from N addition		Strengbom et al. 2002
Boreal forest, Sweden	12	(#)	Increased abundance of the green alga, *Scoliciosporum chlorococcum*, on conifers	Confounding temperature effect	Bråkenhielm and Quinghong 1995
Red spruce High elevation New Hampshire spruce fir forest	<16	#	First year foliage showed lower membrane instability, increased electrolyte losses, greater susceptibility to frost damage	Similar effects were observed after 12 years of fertilization at 15.7 and 31.4 kg N ha^{-1} yr^{-1}, suggesting that the CL is well below 15.7	Schaberg et al. 2002
Norway spruce stand, southern Finland	25	(#)	Decreased biomass of dominant oligotrophic mosses *Pleurozium schreberi* and *Dicranum polysetum*	4 yr study. 30 kg S also added therefore effect not due to N alone	Mäkipää 1998
Pinus-Cladina boreal forest, Ontario, Canada	<40	##	Increase in nitrification (lichen-dominated bedrock) leading to N leaching; increased production of NH_4^+ in tree islands with deeper soils	Hydrological connectivity in taiga ecosystems may permit cascading N saturation in boreal shield landscapes	Lamontagne 1998, Lamontagne and Schiff 1999

Table 6.2—Empirical critical loads of nutrient N for the Taiga ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical load for N deposition *kg ha⁻¹ yr⁻¹*	Reliability	Response	Comments	Study
Lichen, moss, and algae	1-3	#	Changes in alga, bryophyte, and lichen community composition, cover, tissue N or growth rates		Berryman et al. 2004, Berryman and Straker 2008, Geiser et al. 2010, Moore et al. 2004, Poikolainen et al. 1998, Strengbom et al. 2003, Vitt et al. 2003
Mycorrhizal fungi, spruce-fir forests	5-7	(#)	Change in ectomycorrhizal fungi community structure	Expert judgment extrapolated from Marine West Coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008
Shrublands	6	##	Alterations 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, Strengbom et al. 2003

Provisional N critical loads using ectomycorrhizal fungal abundance and diversity as indicators ranged from 5 to 7 kg ha^{-1} yr^{-1}, based on critical loads determined using the same indicators in similar forest types in the Marine West Coast Forests and Northern Forests ecoregions (Chapters 9 and 7; Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008).

Based on reliable estimates from European work described previously and in section 6.5, critical loads for alterations in shrub and grass community composition in the Taiga ecoregion could be set at 6 kg ha^{-1} yr^{-1} (Nordin et al. 2005, Strengbom et al. 2003; Table 6.1). However, the higher European critical loads estimates correspond to the levels of N added in experimental manipulations, which may far exceed the level of N input that would eventually induce a response. As deposition levels exceed 5 to 15 kg N ha^{-1} yr^{-1}, the following become evident: changes in woodland, heath, and peatland communities of vascular plant (especially shrubs and grasses) and mycorrhizal communities; increased foliar nutrient imbalances; and increased susceptibility of vegetation to frost, drought, pathogens and pests. At deposition levels exceeding 15 kg N ha^{-1}, changes in nitrification rates, soil saturation and N leaching can be documented, especially when the N-holding capacity of moss and lichen mats are exceeded.

6.5 Critical Load Data from Europe or from Other Ecoregions

European critical loads for boreal forest ecosystems (Bobbink et al. 2003) as updated by the Alterra Rapport 1382 (de Vries et al. 2007) are 10 to 15 kg N ha^{-1} yr^{-1} for soil processes (increased mineralization, nitrification and N leaching); 10 to 20 kg N ha^{-1} yr^{-1} for increased risk of foliar nutrient imbalances (decreased P, K and Mg to N ratios in foliar tissue) in coniferous and deciduous trees and changes in community composition and of ground vegetation, lichens, and mycorrhizae; and 15 to 25 kg N ha^{-1} yr^{-1} for increased susceptibility to frost, drought, pathogens, and pests, and increases in free algae. Based largely on biodiversity changes documented by Nordin et al. 2005 (see section 6.3), de Vries et al. (2007) recommended decreasing the overall critical load for boreal forests from 10 to 20 (Bobbink et al. 2003) to 5 to 10 kg N ha^{-1} yr^{-1}.

European critical loads (Bobbink et al. 2003) for other taiga ecosystem components are 5 to 10 kg ha^{-1} yr^{-1} for tundra with permafrost, 10 to 15 kg ha^{-1} yr^{-1} for alpine and subalpine scrub without permafrost, and 10 to 20 kg ha^{-1} yr^{-1} for wet and dry heaths. Critical loads for Tundra and Northern Forests ecoregions are especially relevant to tundra-covered areas and large river valley areas of the Taiga ecoregion, respectively. All three ecoregions share some floral and faunal species.

6.6 Future Research Directions and Gaps in Data

Research is needed to confirm that European critical loads and study results are applicable to North America. Long-term studies at low levels of experimentally applied N (i.e., 1 to 5 kg ha^{-1} yr^{-1}) are most needed. Although local Alaskan population and emissions sources are relatively small, regional and trans-Pacific sources of N are increasing with massive energy development projects, industrial expansion, and high latitude population growth. Fire frequency and intensity in boreal ecosystems are increasing with global climate change; fire will continue to be a major regional source of NO_x. Because temperature increases are predicted to be greater in northern latitudes, North American studies are needed to elucidate the interplay between climate change, N volatilization, and N deposition on dry- and wet-land biota, communities, and ecosystems. Indeed, climate change may be the most important driver of vegetation changes in most of the Alaskan portion of the ecoregion, considering the low current background levels of N deposition.

Finally, a greater understanding is needed regarding the underlying mechanisms responsible for N-affected changes, in addition to quantification of the functional relationships between N deposition and specific ecological responses. Such a mechanistic understanding of how N addition alters low N ecosystems could be used to inform modeled predictions.

LITERATURE CITED

Aerts, R.; Chapin, F.S. 2000. **The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns.** Advances in Ecological Research. 30: 1-67.

Allen, E. 2004. **Effects of nitrogen deposition on forests and peatlands: A literature review and discussion of the potential impacts of nitrogen deposition in the Alberta Oil Sands region.** Report to the Wood Buffalo Association. Fort McMurray, AB, Canada: Wood Buffalo Assoc. Available at http://wbea.org/index2.php?option=com_docman&task=doc_view&gid=299&Itemid=104 (Accessed May 10, 2010).

Aronsson, A. 1980. **Frost hardiness in Scots pine. II. Hardiness during winter and spring in young trees of different mineral status.** Studia Forestalia Suecica. 155: 1-27.

Balsberg-Påhlsson, A. 1992. **Influence of nitrogen fertilization on minerals, carbohydrates, amino acids and phenolic compounds in beech (*Fagus sylvatica*) leaves.** Tree Physiology. 10: 93-100.

Berryman, S.; Geiser, L.; Brenner, G. 2004. **Depositional gradients of atmospheric pollutants in the Athabasca Oil Sands region, Alberta, Canada: an analysis of lichen tissue and lichen communities.** Lichen Indicator Pilot Program 2002-2003. Final report to the Terrestrial Environmental Effects Monitoring Science Sub-committee of the Wood Buffalo Environmental Association. Available at http://wbea.org/component/option,com_docman/task,cat_view/gid,29/dir,DESC/order,date/Itemid,104/limit,10/limitstart,0/ (Accessed April 20, 2011).

Berryman , S.; Straker, J. 2008. **Nitrogen loading and terrestrial vegetation—Assessment of existing regional vegetation data and recommendations for future monitoring.** Report to the Cumulative Environmental Management Association (CEMA) NO_x-SO_2 Management Working Group (NSMWG) and Eutrophication Task Group. Sydney, BC, Canada: CE Jones and Associates.

Bobbink, R. 2004. **Plant species richness and the exceedance of empirical nitrogen critical loads: an inventory.** Bilthoven, Utrecht University/RIVM. Report Landscape Ecology.

Bobbink, R.; Ashmore, M.R.; Braun, S.; Fluckiger, W.; van der Wyngaert, I.J.J. 2003. **Empirical nitrogen critical loads for natural and semi-natural ecosystems: 2002 update.** In: Achermann, B.; Bobbink, R., eds. Empirical critical loads for nitrogen. Environmental Documentation 164. Background document for expert workshop on empirical critical loads for nitrogen on semi-natural ecosystems; 2002 November 11-13; Berne, Switzerland: Swiss Agency for the Environment, Forests and Landscape: 143-170.

Bråkenhielm, S.; Quinghong, L. 1995. **Spatial and temporal variability of algal and lichen epiphytes on trees in relation to pollutant deposition in Sweden.** Water, Air and Soil Pollution. 79: 61-74.

Britton, A.J.; Fisher, J.M. 2007. **Interactive effects of nitrogen deposition, fire and grazing on diversity and composition of low-alpine prostrate *Calluna vulgaris* heathland.** Journal of Applied Ecology. 44: 125-135.

Bruteig, I.E. 1993. **The epiphytic lichen *Hypogymnia physodes* as a biomonitor of atmospheric nitrogen and sulphur deposition in Norway.** Environmental Monitoring and Assessment. 26: 27-47.

CEC (Commision for Environmental Cooperation). 1997. **Ecological regions of North America: Toward a common perspective.** Montreal, Canada: Commission for Environmental Cooperation. 71 p. Available at http://www.cec.org/files/pdf/BIODIVERSITY/eco-eng_EN.pdf (Accessed May 24, 2010).

Cornelissen, J. H. C.; Callaghan, T.V.; Alatalo, J.M.; Michelsen, A.; Graglia, E.; Hartley, A.E.; Hik, D.S.; Hobbie, S.E.; Press, M.C.; Robinson, C.H.; Henry, G.H.R.; Shaver, G.R.; Phoenix, G.K.; Jones, D.G.; Jonasson, S.; Chapin, F.S.; Molau, U.; Neill, C.; Lee, J.A.; Melillo, J.M.; Sveinbjornsson, B.; Aerts, R. 2001. **Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass?** Journal of Ecology. 89: 984-994.

Crittenden, P.D. 1998. **Nutrient exchange in an Antarctic macrolichen during summer snowfall-snow melt events.** New Phytologist. 139(4): 697-707.

Crittenden, P.D. 2000. **Aspects of the ecology of mat-forming lichens.** Rangifer. 20(2-3): 127-139.

Crittenden, P.D.; Kalucka, I.; Oliver, E. 1994. **Does nitrogen supply limit the growth of lichens?** Cryptogamic Botany. 4: 143-155.

Curtis, C.J.; Emmett, B.A.; Grant, H.; Kernan, M.; Reynolds, B.; Shilland, E. 2005. **Nitrogen saturation in UK moorlands: the critical role of bryophytes and lichens in determining retention of atmospheric N deposition.** Journal of Applied Ecology. 42: 507-517.

de Vries, W.; Kros, H.; Reinds, G.; Wamelink, W.; Mol, J.; van Dobben, H.; Bobbink, R.; Emmett, B.; Smart, S.; Evans, C.; Schlutow, A.; Kraft,P.; Belyazid, S.; Sverdrup, H.; van Hinsberg, A.; Posch, M.; Hettelingh, J.-P. 2007. **Developments in deriving critical limits and modeling critical loads of nitrogen for terrestrial ecosystems in Europe.** Alterra Report 1382 [Alterra-rapport 1382]. Wageningen, The Netherlands: Wageningen University, Alterra. 206 p.

Emmett, B.A. 2007. **Nitrogen saturation of terrestrial ecosystems: some recent findings and their implications for our conceptual framework.** Water, Air and Soil Pollution. 7: 99-109.

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

Gough, L.; Osenberg, C.W.; Gross, K.L.; Collins, S.L. 2000. **Fertilization effects on species density and primary productivity in herbaceous plant communities.** Oikos. 89: 428-439.

Hall, J. V.; Frayer, W.E.; Wilen, B.O. 1994. **Status of Alaska wetlands.** Anchorage, AK: U.S. Department of the Interior, U.S. Fish and Wildlife Service. 32 p. Available at www.fws.gov/wetlands/_documents/gSandT/StateRegionalReports/Status/AlaskaWetlands.pdf (Accessed March 14, 2011).

Holopainen, T.; Karenlampi, L. 1985. **Characteristic ultrastructural symptoms caused in lichens by experimental exposure to nitrogen compounds and fluorides.** Annales Botanici Fennici. 22: 333-342.

Hyvärinen, M.; Crittenden, P.D. 1998a. **Growth of the cushion-forming lichen, *Cladonia portentosa*, at nitrogen-polluted and unpolluted heathland sites.** Environmental and Experimental Botany. 40: 67-76.

Hyvärinen, M.; Crittenden, P.D. 1998b. **Relationships between atmospheric nitrogen inputs and the vertical nitrogen and phosphorus concentration gradients in the lichen *Cladonia portentosa*.** New Phytologist. 140 (3): 519-530.

Jaffe, D; Zukowski, M.D. 1993. **Nitrate deposition to the Alaskan snowpack.** Atmospheric Environment. 27A: 2935-2941.

Jönsson, A.M. 2000. **Soil treatment effects on bark lesions and frost sensitivity of beech (*Fagus sylvatica*) in southern Sweden.** Forest Ecology and Management. 129:167-175.

Jönsson, A.M.; Ingerslev, M.; Raulund-Rasmussen, K. 2004a. **Frost sensitivity and nutrient status in a fertilized Norway spruce stand in Denmark.** Forest Ecology and Management. 201:199-209.

Jönsson, A.M.; Kivimäenpää, M.; Stjernquist, I.; Sutinen, S. 2001. **Frost hardiness in bark and needles of Norway spruce in southern Sweden.** Trees. 15:171-176.

Jönsson, A.M.; Rosengren-Brinck, U.; Nihlgård, B. 2004b. **Excess nitrogen affects the frost sensitivity of the inner bark of Norway spruce.** Annals of Forestry Science. 61: 293-298.

Kallio, T.K.; Häkkinen, R.; Heinonen, J. 1985. **An outbreak of *Gremmeniella abietina* in central Finland.** European Journal of Forest Pathology. 15: 216-223.

Kellner, P.S.; Redbo-Torstensson, P. 1995. **Effects of elevated nitrogen deposition on the field-layer vegetation in coniferous forests.** Ecological Bulletins. 44: 227-237.

Kytöviita, M.-M.; Crittenden, P.D. 2007. **Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*.** Annals of Botany. 100: 1537-1545.

Lamers, L.P.M.; Bobbink, R.; Roelofs, J.G.M. 2000. **Natural nitrogen filter fails in polluted raised bogs.** Global Change Biology. 6: 583-586.

Lamontagne, S. 1998. **Nitrogen mineralization in upland Precambrian Shield catchments: contrasting the role of lichen-covered bedrock and forested areas.** Biogeochemistry. 41: 53-69.

Lamontagne, S.; Schiff, S.L. 1999. **The response of a heterogeneous upland boreal shield catchment to a short term NO_3^- addition.** Ecosystems. 2: 460-473.

Lamontagne, S.; Schiff, S.L. 2000. **Response of soil microorganisms to an elevated nitrate input in an open *Pinus banksiana-Cladina* forest.** Forest Ecology and Management. 137: 13-22.

Lilleskov, E.A. 1999. **Decline of above- and belowground ectomycorrhizal fungal diversity over an atmospheric nitrogen deposition gradient near Kenai, Alaska.** Ithaca, NY: Cornell University.198 p. Ph.D. dissertation.

Lilleskov, E.A.; Fahey, T.J.; Horton, T.R; Lovett, G.M. 2002. **Belowground ectomycorrhizal fungal community change over a nitrogen deposition gradient in Alaska.** Ecology. 83: 104-115.

Lilleskov, E.A.; Fahey, T.J.; Lovett, G.M. 2001. **Ectomycorrhizal fungal aboveground community change over an atmospheric nitrogen deposition gradient.** Ecological Applications. 11: 397-410.

Lilleskov, E.A.; Wargo, P.M.; Vogt, K.A.; Vogt, D.J. 2008. **Mycorrhizal fungal community relationship to root nitrogen concentration over a regional atmospheric nitrogen deposition gradient in the northeastern US.** Canadian Journal of Forest Research. 38: 1260-1266.

Longton, R.E. 1997. **The role of bryophytes and lichens in polar ecosystems.** In: Woodin, S.J.; Marquiss, M., eds. Ecology of Arctic environments. Oxford, UK: Blackwell Science: 69-96.

Mäkipää, R. 1998. **Sensitivity of understory vegetation to nitrogen and sulfur deposition in a spruce stand.** Ecological Engineering. 10: 87-95.

Moore, T.; Blodau, C.; Turunen, J.; Roulet, N.; Richard, P.J.H. 2004. **Patterns of nitrogen and sulfur accumulation and retention in ombrotrophic bogs, eastern Canada.** Global Change Biology. 11: 356-367.

NADP (National Atmospheric Deposition Program). 2008. **National Atmospheric Deposition Program/ National Trends Network.** Available at http://nadp.sws.uiuc.edu/ (Accessed April 27, 2008).

Näsholm, T.; Ekblad, A.; Nordin, A.; Giesler, R.; Högberg, M; Högberg, P. 1998. **Boreal forest plants take up organic nitrogen.** Nature. 392: 914-916.

Nordin, A.; Näsholm, T.; Ericson, L. 1998. **Effects of simulated N deposition on understorey vegetation of a boreal coniferous forest.** Functional Ecology. 12: 691-699.

Nordin, A.; Högberg, P.; Näsholm, T. 2001. **Soil nitrogen form and plant nitrogen uptake along a boreal forest productivity gradient.** Oecologia. 129: 125-132.

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

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

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

Strengbom, J.; Nordin, A.; Näsholm, T.; Ericson, L. 2002. **Parasitic fungus mediates change in nitrogen-exposed boreal forest vegetation.** Journal of Ecology. 90: 61-67.

Strengbom, J.; Walheim, M.; Näsholm, T.; Ericson, L. 2003. **Regional differences in the occurrence of understory species reflect nitrogen deposition in Swedish forests.** Ambio. 32: 91-97.

Tamm, C.O.; Aronsson, A.; Popovic, B.; Flower-Ellis, J. 1999. **Optimum nutrition and nitrogen saturation in Scots pine stands.** Studia Forestalia Suecica. 209: 1-126.

Vitt, D.H.; Wider, K.; Halsey, L.A.; Turetsky, M. 2003. **Response of *Sphagnum fuscum* to nitrogen deposition: A case study of ombrogenous peatlands in Alberta, Canada.** The Bryologist. 106(2): 235-245.

Walker, T.R.; Crittenden, P.D.; Young, S.D. 2003. **Regional variation in the chemical composition of winter snow pack and terricolous lichens in relation to sources of acid emissions in the Usa River basin, northeast European Russia.** Environmental Pollution. 125: 401-412.

Wieder, R.K.; Vitt, D.H.; Burke-scoll, M.; Scott, K.D.; House, M.; Vile, M.A. 2010. **Nitrogen and sulphur deposition and the growth of *Sphagnum fuscum* in bogs of the Athabasca Oil Sands Region, Alberta.** In: Aherne, J.; Shaw, D.P., guest eds. Impacts of sulphur and nitrogen deposition in western Canada. Journal of Limnology. 69 (Suppl. 1): 161-170.

Wiedermann, M.M,; Nordin, A.; Gunnarsson, U.; Nilsson, M.B.; Ericson, L. 2007. **Global change shifts vegetation and plant-parasite interactions in a boreal mire.** Ecology. 88: 454-464.