5 TUNDRA

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5.1 Ecoregion Description

The North American Arctic, comprising the Tundra and Arctic Cordillera ecoregions (CEC 1997, Chapter 2), covers more than 3 million km^2 (300 million ha), and accounts for nearly 14 percent of the North American land mass. The North American Arctic also constitutes about 20 percent of the much larger circumpolar Arctic shared by Canada, the United States, and six European and Asian countries. The ecoregion description is adapted from CEC (1997). The Tundra ecoregion (CEC 1997, Figure 2.2) is a mosaic of alpine meadows, foothills, mesas, low-lying coastal plains, river corridors, and deltas encompassing northern and western Alaska, the arctic islands of Canada, northern portions of the Yukon and Northwest Territories, and far northern Quebec. Coastal plains are typically wet with high densities of shallow lakes which are covered by ice for 9 months or more. Uplands have fewer, deeper lakes, most of which are connected to river networks draining into the Arctic Ocean or Bering Sea. A key feature is that soils are frozen in spatially contiguous permafrost and often contain large stores of organic carbon (or "peat"). Soil surface layers thaw in summers, usually to a depth of <1 m. The climate is characterized by long, dark, cold winters and short, cool summers with up to several months of daylight. Annual precipitation varies from 10 to 50 cm; snow may fall any month and snow pack usually persists for at least 9 months. Snowfall and its redistribution by winds both influence and are partly determined by plant community structure. The vegetation is characterized by combinations of sedges, grasses, shrubs, bryophytes, lichens, and forbs. Shrubs include dwarf birch (*Betula nana*), willows (*Salix spp.*), and heath species. Moving from south to north, shrub densities typically decrease, and sedges, mosses, and lichens increasingly dominate. River valleys are often lined with tall birch or willow shrubs, and occasionally with small balsam poplar (*Populus balsamifera*) or stunted white and black spruce (*Picea glauca* and *P. mariana*) trees. Wetlands are common in low-lying areas and support sedges and bryophytes.

5.2 Ecosystem Responses to N Deposition

A growing body of literature shows that plant growth, litter and soil organic matter decomposition, primary productivity, ecosystem carbon (C) storage, and plant community composition in arctic tundra ecosystems are at least partly controlled by nitrogen (N) availability and N deposition rates. This is because low N availability limits both microbial decomposition and plant growth in arctic tundra (Robinson and Wookey 1997, Shaver et al. 1992). For example, high rates of N addition can lead to large losses of organic C from tundra peat as well as to increases in vascular plant growth (Mack et al. 2004). Experimental N additions typically increase plant growth in tundra and responses are moderated by environmental factors. Graminoids and shrubs become dominant in dry heath tundra in well drained uplands, shrubs become dominant in moist tundra on gentle slopes, graminoid biomass increases in low-lying wet tundra, and bryophyte (mosses, hornworts, and liverworts) and lichen biomass increases with increasing moisture availability (Shaver et al. 1998, van Wijk et al. 2004). Even though N deposition may increase plant growth and net primary production, increases in peat and soil organic matter decomposition resulting from N deposition could be large enough to offset C accumulation by vegetation, resulting in net C losses from tundra ecosystems (Nowinski et al. 2008).

Bryophytes and lichens (referred to collectively as cryptogams) are of particular concern in the arctic because they regulate tundra water balances and energy balances. Cryptogams, especially sphagnum mosses, can dominate the top layer of tundra; the accumulated necrotic biomass can be a major component of peat, which is highly hygroscopic. In addition, acids and phenolic compounds in cryptogams inhibit decay. The growth and abundances of bryophytes and lichens can be diminished by the direct effects of moderate to high N inputs. In addition, increased growth of competing graminoid and shrub species in response to N inputs can result in shading of low-lying bryophytes and lichens, thereby decreasing cryptogam biomass indirectly, even when cryptogam growth is N limited (Berendse et al. 2001, Bubier et al. 2007, van der Wal et al. 2005). Shifts in cryptogam cover, biomass, morphology, and chemistry; changes in the composition of vegetative communities; and shifts in vegetation growth forms to greater dominance by vascular plants (graminoids and shrubs in particular) are indicators of tundra ecosystem responses to N deposition, as well as to other climate change drivers. Also, changes in cryptogam communities and bryophyte-lichen layer thickness, whether derived from N toxicity, shading from vascular plants, or other factors, can alter tundra soil moisture balances, temperature, and nutrient cycling rates (Gornall et al. 2007).

Aquatic ecosystems are often "first responders" to changes in environmental conditions, as their structure and functionality can be altered by changes in exports of nutrients and organic materials from terrestrial ecosystems within drainage basins. This sensitivity is particularly true in arctic tundra, where shallow depth of soil thaw and short residence times of soil solutions can lead to rapid changes in drainage water chemistry in response to biogeochemical changes in terrestrial ecosystems (Hobbie et al. 1999a, Keller et al. 2007), such as could result from elevated N deposition. Arctic streams are sensitive to N inputs, whether from increased N deposition or from increased decomposition in drainage basins due to warming and deeper soil thaw (Benstead et al. 2005). Evidence is emerging from Canada that diatom communities, nutrient cycling, and sediment formation in arctic lakes are being altered by elevated N deposition (Wolfe et al. 2006). Such studies indicate that N deposition may be altering the functioning of terrestrial as well as aquatic ecosystems in arctic tundra regions over broad scales, even when the effects of N deposition on individual terrestrial communities and ecosystems are undetectable.

5.3 Range of Responses Observed

Similarities among Northern Hemisphere arctic ecosystems in climate, soils, marine influences, hydrology, and vegetation justify the application of Eurasian research to assessments of the North American tundra response to N deposition. The definition of tundra employed by Bobbink et al. (2003) and the UNECE (2007) for Europe is based on the European University Information Systems (EUNIS) system of classification (Davies et al. 2004). 'Tundra' ecosystems share similarities with 'arctic, alpine and subalpine scrub habitats' ecosystems in that the growing season is short, temperatures are low, winds are frequent and strong, and the distribution of plant communities depends on the distribution of snow during winter and spring. Both ecosystem types are influenced by frost activity or solifluction, slow rates of organic matter decomposition and nutrient cycling, and limitation of primary production due to low nutrient availability (Robinson and Wookey 1997). As with North American tundra, the key feature that distinguishes tundra from other ecological regions in both the CEC and EUNIS systems is the presence of permafrost, which restricts deep root penetration and often keeps the overlying thawed soil layer waterlogged in summer. Responses to N deposition are summarized in Table 5.1.

5.3.1 Community Level Responses of Tundra Vegetation

Long-term N addition experiments typically add N at high rates, e.g., 10 to100 kg ha^{-1} yr^{-1}. These rates are one to two orders of magnitude greater than background N deposition rates and well in excess of tundra plant N uptake requirements. Such experiments provide insights into mechanisms of vascular plant responses to atmospheric N deposition but are of limited use in quantifying ecosystem response levels. Growth rates of vascular plant species typically increase in response to experimental N additions in dry, moist, and wet tundra ecosystems in both low and high latitude arctic regions. Because vascular plant species differ in sensitivity to N deposition and N availability, plant community composition typically shifts after several years or decades of experimental N additions. For example, primary productivity increased dramatically in dry heath tundra near Toolik Lake, Alaska, after 8 years of fertilization at 100 kg N ha^{-1} yr^{-1} (Gough et al. 2002). Species richness decreased in this study as dwarf birch, a low-lying shrub, became dominant and various graminoids, shrubs, forbs, and cryptogams declined. Species shifts and primary productivity may increase with N additions in high arctic systems as well. For example, Madan et al. (2007) reported increases in growth and biomass of shrubs (willows and purple mountain saxifrage (*Saxifraga oppositofolia*)) as well as increases in cryptogam cover in Greenland polar deserts (ambient deposition 1 kg N ha^{-1} yr^{-1}) in response to relatively low levels (5 kg N ha^{-1} yr^{-1}) of experimental N addition.

A recent 3-year study in northwest Greenland (Arens et al. 2008) suggests that N addition rates as low as 1 to 5 kg ha^{-1} yr^{-1} (ambient deposition of 0.1 to 5 kg N ha^{-1} yr^{-1}) can dramatically increase photosynthesis and growth of grass species, and significantly alter the structure and function of high arctic systems, particularly with increases in phosphorus (P) availability. The target high arctic ecosystem encompassed dwarf shrubs, graminoids, forbs, bryophytes, and lichens. Measuring carbon dioxide (CO_2) fluxes in a portable field chamber, the authors demonstrated a near doubling of gross ecosystem photosynthesis at plots with 0.5 and 1 kg added N ha^{-1} yr^{-1} after both 1 and 2 years of treatment. The photosynthesis response saturated between 1 and 5 kg added N ha^{-1} yr^{-1}, presumably because P became limiting. Total plant cover followed the same pattern, increasing up to the addition of 1.0 kg N ha^{-1} yr^{-1}, then decreasing or not changing through 5 kg added N ha^{-1} yr^{-1}; grasses invaded much of the bare ground. Cover of deciduous shrubs increased 41 percent in the 0.5 kg N ha^{-1} yr^{-1} treatment, graminoids cover increased 97 percent with the 1 kg N ha^{-1} yr^{-1} treatment, and forb cover increased 296 percent and 740 percent with 1 and 5 kg N ha^{-1} yr^{-1} treatments. Bryophyte and lichen cover appeared to increase to 1 kg N ha^{-1} yr^{-1} and then decrease, but significance was not noted. The N+P treatment (5 kg N ha^{-1} yr^{-1} plus 2.5 kg P ha^{-1} yr^{-1})—produced the greatest responses, including significant increases in cover of alpine fescue (*Festuca brachyphylla*) grass (from 1.3 percent to 43.8 percent), arctic willow (*Salix arctica*) (4.5 percent to 13.8 percent), bryophytes (3 percent to 10.7 percent), alpine chickweed (*Cerastium alpinum*) (0.2 percent to 4.8 percent), the establishment of arctic bluegrass (*Poa arctica*) (from 0 percent to 6.5 percent), significant decreases in total lichen cover (from 8.2 percent to 2.3 percent), and the eradication of purple mountain saxifrage (from 0.8 to 0 percent). Among the three dominant plants (curly sedge [*Carex rupestris*], entireleaf mountain-avens [*Dryas integrifolia*], and arctic willow), foliar N increased linearly through 5 kg ha^{-1} yr^{-1} of added N. These results provide striking evidence of ecologically important increases in ecosystem productivity, vegetative cover, and altered community composition after just 1 to 2 years of very low N additions.

A meta-analysis by van Wijk et al. (2004) showed that vascular plant growth, primary productivity, and biomass of wet and moist tundra ecosystems in mid-arctic regions of Alaska and Scandinavia increased dramatically in experimental nutrient addition plots (N alone and in combination with P and other nutrients). However, increases in shrub growth in moist tundra were greater in Alaska than in Europe and were greater in moist than in wet tundra. Shrub and graminoid growth increased in both regions, but at the expense of forbs and cryptogams. Also, recent work in mid-arctic Alaska suggests that N deposition on non-acidic tundra (with base-rich soils), unlike the more extensive acidic tundra, may not lead to shrub dominance (Gough and Hobbie 2003). In non-acidic tundra types, enhanced graminoid growth will likely diminish the importance of forbs and cryptogam species.

Bryophytes, particularly mosses, can have positive growth responses to atmospheric N deposition because they lack roots and assimilate N and other nutrients almost exclusively via foliar uptake (Salemaa et al. 2008, Solga and Frahm 2006). Thus, where graminoid and shrub species do not overtop mosses and other bryophytes, N deposition could increase plant growth, primary productivity, and moss mat thickness. However, N deposition can also increase tissue turnover and mortality in some arctic mosses (Koranda et al. 2007), and thereby diminish moss cover in some tundra ecosystems. Also, competition by more erect vascular plants can lead to competitive suppression of moss growth and decreases in moss cover even when moss growth is N limited (Klanderud 2008). Positive growth responses of vascular plants to increased N availability can lead to declines in lichen biomass in low- and mid-arctic regions (van Wijk et al. 2004), but probably not in the high arctic (Cornelissen et al. 2001, Madan et al. 2007), where plant cover is typically less than 100 percent of soil surface area.

A seminal, long-term experiment in the high arctic of the Svalbard Islands, Norway, by Gordon et al. (2001) has been used to identify plant responses observed at different N input levels. The experiment involved three common tundra communities dominated by dwarf shrubs (mountain-avens, mountain heather (*Cassiope)*, and willow species) and also characterized by lichens and bryophytes. Background deposition was very low (<1 kg N ha^{-1} yr^{-1}) with N treatments of 0, 10 and 50 kg ha^{-1} yr^{-1} as ammonium nitrate (NH_4NO_3) solution and 0 and 5 kg P ha^{-1} yr^{-1} as potassium dihydrogen phosphate (KH_2PO_4) in five applications per growing season over 8 years. They reported the following:

- Responses were rapid and persistent. Both N and P concentrations in a dicranum moss (*Dicranum scoparium*) and the juniper polytrichum moss (*Polytrichum juniperinum)* increased with each level of nutrient application. Nitrate (NO_3^-) reductase activity decreased in juniper polytrichum at the low N treatment, suggesting N saturation and the potential for nitrate to pass through the bryophyte layer to become available to microbes and higher plants. Composition of the vegetation communities shifted significantly with a notable decrease in lichen cover. Bryophyte productivity increased and persisted 5 years after N additions ceased, suggesting that N (mainly NH_4^+) was strictly conserved in the bryophyte layer and that any reversal of the effect would be slow.
- The P treatment provided unequivocal evidence of partial limitation by P in this ecosystem, with greater response to N when P was applied. Therefore, in tundra systems, critical loads are expected to be lower in ecosystems that are not P-limited. This is especially notable because global warming is expected to increase both N and P availability (currently wet tundra sites are more likely to be P-limited than moist sites with a thinner peat layer, while dry tundra sites are primarily N-limited [Shaver et al. 1998]).

A circumpolar comparison of effects of N deposition and temperature-warming treatments on lichen cover by Cornelissen et al. (2001) included three studies from North America: Chapin et al. (1995), Hik (as reported in Cornelissen et al. 2001), and Hobbie et al. (1999b), and 11 studies from Sweden and Norway. The Cornelissen meta-analysis demonstrated consistent marked decreases in lichen cover with increased N availability and increasing temperature; all N application rates were relatively high, between 40 and 100 kg ha^{-1} yr^{-1} for a minimum of 3 years. In the low arctic and subarctic, this response was attributed to increased shading of lichens by shrubs, which generally reached a taller stature and were more responsive to N fertilization at lower latitudes compared to the high arctic. Although lichens can achieve a net positive photosynthesis rate very rapidly after hydration, they are often light-limited in the Arctic due to low incident radiation (Hahn et al. 1993). Shading, whether from shrubs or fog and cloud cover, significantly reduces lichen growth rates. Lichen cover responses in the high arctic were more ambiguous, with some studies showing slight increases and others small decreases. Cornelissen (2001) concluded that tundra lichens in climatically milder arctic ecosystems may decline with global climate change because higher temperatures are associated with greater availability of N and P, all of which favor vascular plants.

In addition to the above three North American studies, a study was conducted by Weiss et al. (2005) at the Toolik Lake Tundra LTER site (Alaska), in the northern foothills of the Brooks Range. They documented an essential absence of lichens after 10+ years of fertilization at 100 kg N ha^{-1} yr^{-1}. Phosphorus fertilization at 50 and 100 kg ha^{-1} yr^{-1} improved N_2 fixation rates of the felt lichens, *Peltigera apthosa* and *P. polydactylon*, but the effect was unimportant compared to the reduction in lichen cover.

Since the Bobbink et al. (2003) assessment, a number of studies have provided further insight regarding the effects of N and P availability on tundra vegetation. During a 10-year experiment, Fremstad et al. (2005) tested species cover in low alpine and middle alpine vegetation communities in the Dover Mountains of south-central Norway. Nitrogen was added at 7, 35, and

70 kg ha^{-1} yr^{-1}; background N deposition was 2 to 4 kg ha^{-1} yr^{-1}. The most sensitive species at the warmer, low-alpine site were a witch's hair lichen (*Alectoria nigricans*) and a cetraria lichen (*Cetraria ericetorum*). These species exhibited significant decreases in cover at the lowest N application rate of 7 kg ha^{-1} yr^{-1}. Cover of other witch's hair *(Alectoria ochroleuca*), cetraria (*Flavocetraria cucullata, F. nivalis*), and reindeer (*Cladonia mitis, C. rangiferina, C. stellaris*) lichens decreased at the application rate of 35 kg N ha^{-1} yr^{-1}. The only lichen unaffected by any level of N application was the N_2-fixing snow lichen, *Stereocaulon paschale*. In contrast, fertilization had no significant effect on the bryophytes or vascular plants (dwarf shrubs and graminoids) except for sheep fescue (*Festuca ovina)*, a grass, which increased slightly. At the colder, mid-alpine site, a cetraria lichen (*Cetrariella delisei*), was the only species in which cover changed over 10 years due to N application, and then only at the addition rate of 70 kg ha^{-1} yr^{-1}, implying a slower response time in colder climates.

5.3.2 Physiological and Chemical Responses of Vegetation

The adaptation of arctic vegetation, especially lichens and bryophytes, to N-limited ecosystems through extreme conservation has been well illustrated recently by two studies employing ^{15}N as a tracer. Tye et al. (2005) conducted one-time additions of 1 or 5 kg ^{15}N ha^{-1}, using separate applications of ^{15}N-labeled sodium nitrate ($NaNO_3$) and ammonium chloride (NH_4Cl) at both levels of N addition, in addition to the background deposition rate of 1 kg N ha^{-1} yr^{-1} at two sites in the high arctic tundra of Svalbard, Norway. They observed a highly conservative retention by soil, litter, and vegetation of ~60 percent of both N ions of the initial application across all 3 years. On a unit weight basis, the lichens and graminoids were especially good scavengers of ^{15}N and exhibited a high capacity to immobilize additional N released compared to other sinks (microbes, vascular plants, mosses, willows, litter, humus, mineral soils), although the bulk of ^{15}N was stored in humic and mineral fractions of the soil and in bryophytes. Kytöviita and Crittenden (2007), in a study of lichen mats dominated by reindeer and snow lichens (*Cladonia* and *Stereocaulon*) in a dry boreal forest of Finland, demonstrated that a significant portion of ^{15}N fed to the lower parts of lichens is translocated towards growing apices. They concluded that internal recycling of N improves N use efficiency in lichens and is likely ecologically important in N-limited environments typical of the undisturbed arctic. These and other studies have repeatedly shown a direct correlation between N application or N availability and concentrations of N in lichen thalli (Hahn et al. 1993; Hyvärinen and Crittenden 1998a, 1998b; Hyvarinen et al. 2003; Walker et al. 2003; Weiss et al. 2005).

In addition to decreases in lichen cover with increasing N availability, mostly at relatively high application rates, new evidence points to clear but more subtle effects of low rates of N application (3 to 10 kg ha^{-1} yr^{-1}) on lichen physiology. Makkonen et al. (2007) showed the vulnerability of normally N- and P-limited lichens to nutrient enrichment. Lichen cushions of the star reindeer lichen (*Cladonia stellaris*) were treated with 3 and 10 kg N ha^{-1} yr^{-1} and 10 kg P ha^{-1} yr^{-1}, alone and in combination, over 14 weeks. Nitrogen, P, and N:P ratios influenced the proportion of the medullary layer volume occupied by the algal cells, the thallus volume occupied by the internal lumen, and the algal cell-wall area covered by fungal hyphae, indicating that ecologically realistic changes in the availability of key macronutrients can alter the growth of symbionts. Hyvärinen et al. (2003) showed that a moderate N treatment (3 kg ha^{-1} against a background of 0.5 kg ha^{-1} wet deposition in 3 months) lowered usnic acid ($C_{18}H_{16}O_7$) concentrations in the star reindeer lichen with and without P application; P alone increased usnic acid, and higher N (10 kg ha^{-1}) had no effect on usnic acid. None of the treatments increased growth rate. Usnic acid in lichens has well established anti-microbial and UV-β protection properties (Rikkinen 1995) relating to lichen fitness. By inhibiting catalysis of urea to carbon dioxide (CO_2) and ammonia (NH_3), usnic acid likely moderates metabolic imbalances in lichens created by excess C and insufficient N (Rikkinen 1995).

Sundberg et al. (2001), in an elegant study of lichen transplants, demonstrated the highly regulated, species-specific balance of C and N for coordinated development of lichen thalli. Nitrogen availability to transplants of the arctic kidney lichen (*Nephroma* *arcticum*) and a felt lichen (*Peltigera aphthosa*) was manipulated during 4 summer months by removing cyanobacterial N_2-fixing structures to cause N starvation, or by weekly irrigation with NH_4NO_3 at a rate of 9 kg N ha^{-1} yr^{-1} plus background deposition of 5 kg ha^{-1} yr^{-1}. N-starved lichens continued to gain weight, but did not increase in cover, demonstrating that C-fixation can proceed under N-limited conditions, although N is required for hyphal growth. Cover of lichens with added N increased more slowly than nonfertilized controls. For all treatments, weight gain was dependent on the proportion of N invested in algal photosynthetic tissue and there was a positive correlation between light use efficiency and thallus N. Intra-specific ratios of chlorophyll *a*:chitin (an N-containing polysaccharide in cell walls) and chlorophyll *a*:ergosterol (an N-containing component of cell membranes in fungi and algae) were relatively constant across a two- to threefold variation in thallus N, suggesting that lichens regulate N distribution within the thallus.

5.4 Critical Loads Estimate

We have few experiments assessing the effects of N additions at our proposed critical load for the North American Tundra ecoregion. There is only one published study specific to the North American Tundra ecoregion (Arens et al. 2008) that has used ecologically realistic N input rates to suggest vascular plant, bryophyte, or lichen-based critical loads (see Table 5.1). Critical loads are summarized in Table 5.2.

In 2003, the empirically derived critical load for tundra ecosystems in Europe proposed by Bobbink et al. (2003) and adopted by the UNECE (2007) was 5 to 10 kg N ha^{-1} yr^{-1}. This range was considered reliable, even though it is based primarily on one long-term experiment in the high arctic of the Svalbard Islands, Norway, by Gordon et al. (2001). This study is compelling because it included the critical load range, involved controlled additions of N, and looked at responses over an 8-year period (Table 5.1). Data from Fremstad et al. (2005) and Madan et al. (2007), which demonstrated vegetation community responses at 9 to 11 and 6 kg N ha^{-1} yr^{-1}, respectively, corroborate the research by Gordon et al. (2001) and point to the important mediating role of other environmental and genetic factors in cryptogam and vascular plant responses to N deposition. In particular, harsher climates and intrinsic properties of individual species may slow the rate of, or override, responses.

European analyses suggest critical loads not exceed 5 to 10 kg N ha^{-1} yr^{-1}, but the long-term effects of deposition rates lower than 5 kg N ha^{-1} yr^{-1} on tundra ecosystems have not yet been adequately assessed. Recent work, however, suggests arctic systems may respond to rates of N deposition between 1 and 5 kg ha^{-1} yr^{-1} with altered gross photosynthetic productivity, structure, and function of plant communities (Arens et al. 2008). Background N deposition rates in European tundra are higher than N deposition in relatively less polluted regions of the North American Arctic. For example, precipitation chemistry measurements at the Toolik Lake Arctic Tundra LTER site in northern Alaska (Hobara et al. 2006, Shaver[5]) and at NADP sites elsewhere in Alaska (See Chapter 6, and data from Ambler, Alaska, at http://nadp.sws.uiuc.edu/ads/2004/AK99.pdf) show that inorganic N inputs from the atmosphere are <0.5 kg N ha^{-1} yr^{-1}.

Given the multiple lines of evidence from Arens et al. (2008) that deposition as low as 1 kg N ha^{-1} yr^{-1} can impact tundra ecosystems, setting critical loads at 10 to 20 times current N deposition rates measured at relatively pristine tundra sites would be unwise. Aquatic systems in arctic drainages (Wolfe et al. 2006) and indicator species among the shrubs, grasses, lichens, and mosses appear to be responding to N deposition at low levels of ambient atmospheric or experimental N inputs. Cellular ultrastructure and pigment production are sensitive to deposition loading of ≤3 kg N ha^{-1} yr^{-1} (Hyvärinen et al. 2003, Makkonen et al. 2007). Moreover, vegetation in tundra ecosystems is highly efficient with respect to N cycling (Chapin et al. 1980), with plant N uptake from soil ranging between 1 to 6 kg ha^{-1} yr^{-1}, or 20 to 25 percent of the 5 to 20 kg N used to supply annual primary productivity (Shaver et al. 1991,

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[5] Shaver, G.R. Unpublished data. Senior scientist of Marine Biological Laboratory, Ecosystems Center, Woods Hole, MA 02543.

Table 5.1—Responses to N deposition for the Tundra ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Site	N input *kg ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
NW Greenland	1-5	##	Increased net CO$_2$ uptake by combined vegetation saturating at 1.5 kg N ha^{-1} yr^{-1}; changes in shrub, graminoid, forb, bryophyte, and lichen diversity and cover; increased grass cover, increased foliar N	Response is greater if P availability increases	Arens et al. 2008
Hailuota Island, northern Finland, 65° N	<3	(#)	Decreased usnic acid concentrations in lichens at 3 kg; no effect at 10 kg (concave response)	3 kg ha^{-1} on background of 0.5 kg ha^{-1} for 3 months. P increased usnic acid	Hyvärinen et al. 2003
Hailuota Island, northern Finland, 65° N	3 to 10	(#)	Increase in lichen N concentrations, reduction in medullary volume, increase in internal lumen volume	14 week addition of 3 and 10 Kg N (total) and 10 kg P to lichen cushion transplants; P moderated N response	Makkonen et al. 2007
Greenland polar deserts	6	##	Increases in shrub and cryptogam growth and biomass	N addition of 5 kg ha^{-1} yr^{-1}, plus 1 kg ha^{-1} yr^{-1} deposition	Madan et al. 2007
Dover Mtns, south-central Norway 60 ° N	<9-11	##	Decreased lichen cover and increased grass cover at warmer but not colder site	10 yr experimental addition of N at 7, 35 and 70 kg ha^{-1} yr^{-1} to low and mid alpine vegetation, plus 2 to 4 kg N ha^{-1} yr^{-1} deposition	Fremstad et al. 2005
Svalbard Islands, Norway 78 ° N	<10	##	Increased N and P concentrations in cryptogams, reduced nitrate reductase activity in bryophytes, N saturation of cryptogam layer, decrease in lichen cover, and increase in bryophyte cover	8 yr addition of 0, 10 and 50 kg N ha^{-1} yr^{-1}; 0 and 5 kg P ha^{-1} yr^{-1} to three high arctic vegetation types. Adding P exacerbated adverse N effects. Wet tundra (P limited) may have higher critical loads than dry tundra (N limited)	Gordon et al. 2001
Västerbotten, Sweden 66.2° N (collected); Ulterviken, Sweden 63.5° N (transplanted)	<14	#	Increased lichen N concentrations; slightly slowed growth in cover area; increase in chlorophyll a, ergosterol, and chitin	Comparison of N starved (cephalodia removed), control and 10 kg ha^{-1} yr^{-1} N to N$_2$-fixing lichens. After 4 months fertilization appeared to mostly benefit lichens, which were N-limited	Sundberg et al. 2001
Circumpolar arctic	<40	#	Increased growth of shrubs, decrease in lichen cover (attributed to shading by shrubs)	Meta-analysis of 14 arctic studies. Responses diminish with latitude due to colder temps and poorer N and P mobilization	Cornelissen et al. 2001
Toolik Lake tundra LTER, Brooks Range, Alaska 66° N	<50	##	Decreased cover and species diversity of lichens	Lichens disappeared after 10 years fertilization at 100 kg ha^{-1} yr^{-1}	Weiss et al. 2005

Table 5.2—Empirical critical loads of nutrient N for the Tundra ecoregion. Reliability rating: ## reliable; # fairly reliable; (#) expert judgment

Ecosystem component	Critical Load for N deposition *kg ha⁻¹ yr⁻¹*	Reliability	Response	Comments	Study
Tundra: herbs	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
Tundra: cryptogams	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, Hyvärinen et al. 2003, Makkonen et al. 2007

Shaver and Chapin 1991). Nitrogen deposition rates equal to or in excess of annual plant N uptake would likely alter competitive interactions among plant species, dominant growth forms, biogeochemical exports, and energy balances of tundra ecosystems. Given the high degree of N limitation of plant growth in the North American Tundra ecoregion, low background levels of N deposition in historic and geological time, low levels of N cycling between tundra plants and soils, and the apparent sensitivity of freshwater ecosystems in the Arctic to changes in landscape biogeochemistry, the North American Tundra ecoregion critical load for N deposition should considerably lower than the European tundra critical load. We recommend that the critical load for the North American Tundra ecoregion be 1 to 3 kg N ha^{-1} yr^{-1}; the lower value is two times estimates for inorganic N deposition in Alaskan tundra monitoring sites. We consider this critical load to be reliable, but note that it is primarily supported by work in a single high arctic location in North America (Arens 2008).

5.5 Future Research Directions and Gaps in Data

A more extensive network of atmospheric deposition monitoring stations is clearly needed in the North American Tundra ecoregion. These monitoring stations should focus on acquiring high quality, year-round measurements of inorganic, particulate, and organic N forms as well as other biologically active elements including S, mercury (Hg), calcium (Ca), magnesium (Mg), and potassium (K). Further research is needed, specifically in North American tundra locations outside of Greenland, in both high and low arctic environments. This research should compare ecologically realistic applied, measured, or modeled N deposition with biogeochemical responses to N deposition, with physiological/morphological/distribution data for various indicator vascular plant, bryophyte and lichen species, and with foliar or thallus N concentrations. Until then, critical loads based on responses from Nordic countries will remain our best estimates.

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