Review paper

Topography as a key factor driving atmospheric nitrogen exchanges in arctic terrestrial ecosystems

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Identifying the key drivers of nitrogen cycling processes that influence gaseous N exchanges in arctic ecosystems is essential for predicting the response of northern systems to changes in climatic conditions. In this review we examine pathways of N input (atmospheric N deposition and biological N2-fixation), cycling (N mineralization, immobilization and nitrification) and output (denitrification and nitrifier denitrification) found across the Arctic with a focus upon gaseous N exchanges in these ecosystems. Cyanobacteria are ubiquitous in the Arctic where they can be found in association with lichen or bryophytes and also as free-living components of biological soil crusts. N2-fixation by cyanobacteria in arctic ecosystems provides significant landscape-scale N inputs, and is an important N source for annual plant N uptake. The activity and extent of these cyanobacterial associations is driven primarily by moisture gradients associated with topography that determine nutrient availability. N2-fixation rates tend to be highest in relatively low topographical or microtopographical positions that are associated with soils of higher total N, mineralizable N, total carbon and organic carbon compared to higher topographical positions. Topography is also a key landscape-level driver of N mineralization, nitrification and denitrification processes through its control on factors such as soil moisture, soil temperature and nutrient availability. In general, while N mineralization rates are also higher in relatively low topographical or microtopographical positions, net immobilization and immobilization tend to be inhibited in these locations. This higher mineralization is linked to relatively high N2O emissions in lower lying areas in arctic landscapes since moisture and NH4 levels tend to be higher in those locations and are important controls on denitrification and nitrifier denitrification respectively. These soil topographical controls are modulated by arctic plants which may also have a direct, light-dependent role in N2O emissions, and undoubtedly play important indirect roles in gaseous N cycling via evapotranspiration effects. Our review indicates that arctic microscale and field topographic variation dominate patterns of atmospheric N inputs and losses in arctic ecosystems. However, further studies are needed to provide a better understanding of the associated driving factors on the multitude of processes that influence gaseous N exchange.

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1. Introduction

Plant productivity in the Arctic is limited both by low soil temperatures and soil moisture, but during the growing season the availability of soil nutrients (principally nitrogen (N) and phosphorus (P)) is the primary factor limiting plant growth (Shaver and Chapin, 1980; Chapin et al., 1995; Jonasson et al., 1999a,b; Zamin and Grogan, 2012). Soil nutrients vary with both depth and topography across arctic landscapes leading to variation in total N, NH4, NO3 and NO2 and PO4 (Giblin et al., 1991; Paré and Bedard-Haughn, 2012). Variation in soil nitrogen availability is a key determinant of plant community structure (McKane et al., 2002). Different vegetation communities, in turn, give rise to differences in greenhouse gas emissions (including N2O) through their influence on soil microbial processes (Stewart et al., 2012a; Brumwell et al., 2012). Arctic ecosystems appear to be more
and uptake of organic N from N2-fixers: Arctic tundra (0.2 kg N ha\(^{-1}\) y\(^{-1}\)) and Boreal forest (0.5 kg N ha\(^{-1}\) y\(^{-1}\)). Furthermore, establishing key drivers in various nutrient cycling processes is also essential for predicting the biogeochemical responses of arctic systems to changes in climatic conditions. Much research has focussed on the pathways for internal cycling of N and P in arctic systems because it is well established that these are the major determinants of plant nutrient supply. However, there is still a lack of knowledge surrounding the importance of the various pathways and key factors that drive inputs and losses of gaseous N in arctic landscapes, but much can be inferred from the extensive N work performed in other ecosystems. In this review, we will synthesize current knowledge on pathways of atmospheric N inputs (from N2 gas that is biologically fixed, as well as wet and dry N deposition), cycling (N mineralization, immobilization and nitrification) and outputs (gaseous N losses due to denitrification and nitrifier denitrification). We will examine the abiotic and biotic factors that drive these processes and explore how these factors are related to landscape features in arctic ecosystems. Finally, we will identify the major gaps in our knowledge of atmospheric N exchange that need to be addressed to fully understand the functioning of arctic terrestrial ecosystems and how they may respond to climate change.

2. Biological N fixation and atmogenic N deposition

Biological N\(_2\)-fixation is the primary source of new N input in many arctic ecosystems (Fig. 1; pathway a) providing an estimated 30–80% of total landscape annual N inputs (Henry and Svoboda, 1986; Chapin and Bledsoe, 1992; Hobara et al., 2006; Solheim et al., 2006; Stewart et al., 2011a). As might be expected, average rates of N\(_2\)-fixation are low compared with lower latitude ecosystems: Arctic tundra (0.2–2 kg N ha\(^{-1}\) y\(^{-1}\)), Boreal forest (0.1–4 kg N ha\(^{-1}\) y\(^{-1}\)), Temperate forest (0.1–15 kg N ha\(^{-1}\) y\(^{-1}\)), Grassland (0.5–8.2 kg N ha\(^{-1}\) y\(^{-1}\)) and Tropical forest (5–100 kg N ha\(^{-1}\) y\(^{-1}\)) (Boring et al., 1988; Chapin and Bledsoe, 1992; Reed et al., 2011). Although overall landscape level N inputs via biological N\(_2\)-fixation may be relatively low in arctic environments, some N\(_2\)-fixing organisms, particularly lichens, have very high rates of N\(_2\)-fixation (Hobara et al., 2006; Stewart et al., 2011a,b,c) and therefore localised inputs can be very significant, and undoubtedly contribute to patchiness in fertility across the landscape.

Atmospheric N deposition inputs are also generally thought to be low compared to other ecosystems; however, while some studies suggest that arctic N deposition ranges from 0.03 to 0.56 kg N ha\(^{-1}\) y\(^{-1}\) (Barsdate and Alexander, 1975; Van Cleve and Alexander, 1981; Gunther, 1989; Shaver et al., 1992; Woodin, 1997; Hodson et al., 2005; Solheim et al., 2006; Aren et al., 2008), other studies suggest that arctic N deposition ranges from 1 to 10 kg ha\(^{-1}\) y\(^{-1}\) (Jaffe and Zukowski, 1993; Gordin et al., 2001; Lagerström et al., 2007) or may be as high as 50 kg ha\(^{-1}\) y\(^{-1}\) (NAPD, 2002; Kitzler et al., 2006) (Fig. 1; pathway b). In many arctic ecosystems N inputs via biological N\(_2\)-fixation may be far greater than atmospheric N deposition inputs; however in others, N deposition may exceed or even limit N inputs from biological N\(_2\)-fixation (DeLuca et al., 2008). Therefore, variation in wet and dry atmospheric N deposition needs to be considered in evaluating the relative importance of N inputs via N\(_2\)-fixation in arctic ecosystems. Both arctic and subarctic experimental studies have shown that addition of NH\(_4\) can inhibit N\(_2\)-fixation in both Nostoc sp. and lichens and weak correlations between naturally occurring soil NH\(_4\) levels and N\(_2\)-fixation have been observed (Kallio, 1978; Chapin and Bledsoe, 1992). The declining gradient in atmospheric N deposition with increasing latitude may be one reason why there is relatively high N\(_2\)-fixation rates at more northerly latitudes in the boreal forests of Fennoscandia (59°–69°) (Phil-Karlsson et al., 2003; Zackrisson et al., 2009). However, the influence of ambient mineral N levels on tundra N\(_2\)-fixation has yet to be determined and requires further study.

3. N\(_2\)-fixing organisms in the Arctic

Cyanobacteria are ubiquitous in the Arctic where they are the primary source of newly fixed N in these nutrient-poor ecosystems (Alexander and Schell, 1973; Alexander, 1974; Granhall and Lid-Torsvik, 1975; Davey, 1983; Henry and Svoboda, 1986; Chapin et al., 1991; Chapin and Bledsoe, 1992; Liengen, 1999a; Hobara et al., 2006; Solheim et al., 2006). There is a high diversity of cyanobacterial species in the Arctic and in several ecosystems they can be the dominant microorganisms both in terms of biomass and productivity (Vincent, 2000; Zielke et al., 2005). Globally, N\(_2\)-fixers can be autotrophic, heterotrophic, chemolithotrophic, photo-heterotrophic and methanogenic (Reed et al., 2011) with most N\(_2\)-fixation in arctic environments carried out near, on, or above the soil surface by phototrophic cyanobacteria. In contrast to temperate systems, N\(_2\)-fixation by rhizosphere and free-living diazotrophic

![Fig. 1. N input, cycling and output pathways influencing gaseous N exchange in arctic ecosystems including surface biological N\(_2\)-fixation (a), atmospheric deposition (b), release and uptake of organic N from N\(_2\)-fixers (c), vascular plant uptake of inorganic N (d), vascular plant uptake of organic N (e), inorganic N as a source of substrate for denitrification and nitrifier denitrification (f), Gaseous N emissions from the soil (g), N\(_2\)O flux from plants via evapotranspiration and passive pathways (h), and N\(_2\)O flux in the rhizosphere (i).](https://example.com/fig1.png)
soil bacteria deeper in the soil profile is negligible (Jordan et al., 1978; Chapin et al., 1991; Solheim et al., 1996).

In addition to symbiotic and epiphytic associations, free-living cyanobacterial associations also occur as a component of biological soil crusts (BSCs) along with other bacteria, algae, mosses, liverworts, fungi and lichens. Cyanobacterial species such as *Nostoc* spp., that form both free-living colonies on the soil surface and grow epiphytically on bryophytes are perhaps the most important contributors to N₂-fixation in both arctic and antarctic environments (Fogg and Stewart, 1968; Alexander, 1974; Davey, 1983; Henry and Svoboda, 1986; Lennihan and Dickson, 1989; Chapin and Bledsoe, 1992; Solheim et al., 1996; Zielke et al., 2005; Stewart et al., 2011a, 2011b). These BSCs also play an essential role in stabilizing soil substrates and in nutrient cycling (Eldridge, 1998; Issa et al., 2001, 2007; Hu et al., 2003; Veluci et al., 2006). Cyanobacterial symbioses with lichens play a large role in mediating N inputs via N₂-fixation in the Arctic (Schell and Alexander, 1973; Kallio and Kallio, 1975; Crittenden and Kershaw, 1978; Gunther, 1989). Lichen species are particularly well adapted to extreme environmental conditions and are often the dominant vegetation cover in barren arctic habitats where vascular plants maintain much of their biomass below the surface or are unable to establish (Tenhunen et al., 1992; Kurina and Vitések, 1999). *Stereocaulon* spp., *Peltigera* spp. and *Nephroma arcticum* are common cyanolichens in arctic ecosystems and have N₂-fixation rates often exceeding that of other cyanobacterial symbioses (Alexander and Schell, 1973; Hobara et al., 2006). For example, *Stereocaulon paschale* had rates of N₂-fixation per unit ground cover (24.9 kg N ha⁻¹ yr⁻¹) that were approximately 5 times higher than BSCs within a low arctic tundra landscape (Stewart et al., 2011a). However, despite the higher rates associated with lichens, total N inputs from lichens may be limited due to relatively low spatial coverage across the landscape compared with BSCs and mosses, as well as the limited time when lichens have adequate moisture conditions to allow for active N₂-fixation (Fig. 2).

Bryophytes influence N₂-fixation in many ecosystems by forming facultative associations with cyanobionts (DeLuca et al., 2002; Turetsky, 2003). *Pleurozium schreberi*, *Hylomciun splendens*, *Bynum* spp., *Sphagnum* spp., *Racomitrium lanuginosum*, *Jamesoniella colorata*, * Ditrichum strictum*, *Clasmatocolea humilis* and *Anthoceros punctatus* are just a few of the bryophyte species that form associations with cyanobacteria (Turetsky, 2003). Cyanobacteria in association with bryophytes can be epiphytic or endophytic and can reside in a number of different localities including gametophyte cavities and leaf crevices or margins (Granhall and Selander, 1973; Rai et al., 2000; Turetsky, 2003). Cyanobacteria found in association with bryophytes may gain a supply of carbohydrates as well as protection against desiccation and UV-radiation, and bryophytes may in turn gain fixed N (Zielke et al., 2005). Moss-associated cyanobacteria alone can provide 2–58% of N in arctic ecosystems (Dodds et al., 1995; Solheim et al., 2006) and while variation is often high within and between bryophyte species, several studies found that the highest levels of N input in arctic landscapes are associated with cyanobacterial moss associations (Alexander and Schell, 1973; Henry and Svoboda, 1986; Solheim et al., 1996; Stewart et al., 2011a, 2011b).

Symbiotic bacteria in associations with vascular plants are not as common as the cyanobacterial associations described above (Gunther, 1989; Solheim et al., 2006). Nevertheless, symbioses between legumes (e.g. *Oxytropsis* spp. and *Astragalus* spp.) and *Rhizobium*-type bacterial root nodules, as well as between *Dysas* spp. and *Frankia*-type bacterial root nodules, as well as between bacterial N₂-fixing associations and *Carex* spp. do occur (Alexander and Schell, 1973; Alexander et al., 1978; Karagatzides et al., 1985; Henry and Svoboda, 1986; Gunther, 1989). In low arctic alpine tundra, N₂-fixation by *Oxytropsis* spp. and *Dysas octopetala* can be high on a plant dry weight basis (~2 µg N per mg plant dry wt⁻¹ day⁻¹), but their overall significance is small because these plants constitute a very small fraction of total ecosystem biomass (Alexander et al., 1978). The recent

![Fig. 2. Nitrogen fixation in an arctic tundra landscape at Daring Lake, NWT. The three main nitrogen fixing associations (*Stereocaulon paschale*, Biological Soil Crusts and *Sphagnum* spp.) are given with their mean growing season N₂-fixation rate under field conditions (below photograph). Arrows indicate the relative contribution of each nitrogen fixing associations based on the mean N₂-fixation rate and areal extent in either Xerophytic Herb Tundra ecosystems that occur at upslope positions or Wet Sedge Meadow ecosystems that occur at lower slope positions. Total N input per hectare per year is also given for each ecosystem. See Stewart et al. (2011a) for further details.](image-url)
increases in shrub growth and cover in the Alaskan Arctic and Mackenzie Delta have been largely attributed to *Alnus* spp. (Tape et al., 2006, 2012; Lantz et al., 2010), which can form a N₂-fixing symbiotic relationship with *Frankia* bacteria, suggesting that the particular success of this species compared to Birch and Willow in these regions may be linked to its capacity to enhance its N supply. Clearly, N inputs via symbiotic associations with vascular plant species may be substantial in the localised patches where they occur, but at landscape and larger scales, N inputs via cyanobacteria are likely to far exceed these inputs in terms of total magnitude (Chapin and Bledsoe, 1992).

The nitrogenase enzyme is responsible for N₂-fixation and is encoded by *nifH*, *nifK* and *nifH* genes (Zehr et al., 2003). Due to the high number of gene products required for the structure, regulation and assembly of nitrogenase, gene expression is highly regulated and transcription of the *nifHDK* operon is a good marker for N₂-fixing conditions (Zehr et al., 2003). All N₂-fixing associations are strongly affected by the properties and requirements of the nitrogenase enzyme (Reed et al., 2011). Activity of the enzyme is controlled by O₂ sensitivity (Robson and Postgate, 1980; Hill, 1988; Reed et al., 2011), response to metal content (Fe, Mo, V, Co, Ca, Mg) (Piccioni and Mauzerall, 1978; Onek and Smith, 1992; Gallon, 1992; Liengen and Olsen, 1997a,b; Hartley and Schlesinger, 2002; Bellenger et al., 2011; Reed et al., 2011) and non-metallic nutrients (C, N, P) (Gutschick, 1981; Vitousek and Howarth, 1991; Chapin et al., 1991; Smith, 1992; Marschner, 1995; Kurina and Vitousek, 2001; Poly et al., 2001), a need for supplies of reducing power and adenosine triphosphate (ATP) (Layzell, 1990; Nash, 1996; Hartley and Schlesinger, 2002; Solheim et al., 2006; Reed et al., 2011), as well as, potential suppression by N availability (Alexander et al., 1978; Chapin et al., 1991; Liengen, 1999a; Phil-Karlsso et al., 2003; Weiss et al., 2005; DeLuca et al., 2008; Zackrissen et al., 2009; DeLuca et al., 2008).

Very few studies have investigated *nifH* gene distribution or activity in terrestrial arctic environments. Deslippe and Egger (2006) provided the first examination of *nifH* diversity of arctic plant-associated soil microbes and found evidence that plants select for different *nif* gene-based diazotrophic communities; however, low sequence identity with known *nifH* sequences indicated that *nifH* gene diversity in polar plant communities is largely unknown. Site factors including plant community composition, soil characteristics, moisture and temperature are the main determinants of *nifH* community structure (Walker et al., 2008). The response of the *nifH* communities to warming in arctic environments does not appear to be consistent across vegetation communities with the strongest response occurring in very wet (hydric) sites, such as wet sedge meadows (Walker et al., 2008), Stewart et al. (2011c) examined *nifH* prevalence in relation to rates of N₂-fixation in mesic birch hummock-hollow ecosystems and found that not only were BSCs significant point sources of N input in these systems, but variation in *nifH* abundance was related to micro-topographical gradients. Hollow BSCs had higher growing season N₂-fixation rates, higher growing season *nifH* abundance, higher total % N and δ¹⁵N values closer to that of atmospheric N₂, all of which suggest that N₂-fixation inputs are larger in the hollows of hummock-hollow ecosystems.

4. Environmental controls on N₂-fixation

N₂-fixation rates at any location depend on the distribution of N₂-fixing biomass and various abiotic variables that influence nitrogenase activity (Gersper et al., 1980). In our review of all the arctic nitrogen fixation studies we could find (Table 1), we conclude that N₂-fixation rates are generally promoted by increases in soil moisture, temperature and light levels (Chapin et al., 1991; Lennihan et al., 1994; Nash and Olafsen, 1995; Liengen and Olsen,

### Table 1

Factors influencing biological N₂-fixation in arctic ecosystems. For each study an increase (+) or decrease (−) in nitrogen fixation is shown for each climate, physiographical or chemical factor. Percentages of increase or decrease are given for studies where values or means were given. Ranges of percentages were calculated by comparing values or means with the most extreme to least extreme difference.

<table>
<thead>
<tr>
<th>Ecosystem type</th>
<th>Location</th>
<th>Study</th>
<th>Precipitation (%)</th>
<th>Temperature (%)</th>
<th>Light (%)</th>
<th>N₂-fixation downslope (%)</th>
<th>Higher N, C, pH (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal-arctic forest,</td>
<td>69°45'N, 27°01'W</td>
<td>Alexander and Schell, 1973; Schell and Alexander, 1973;</td>
<td>+</td>
<td>+</td>
<td>+23</td>
<td>+ MT 17,</td>
<td>+</td>
</tr>
<tr>
<td>Tundra</td>
<td>71°20'N 156°38'W</td>
<td>Alexander et al., 1978</td>
<td>+</td>
<td>OT 16–20</td>
<td>+</td>
<td>+ pH</td>
<td>+</td>
</tr>
<tr>
<td>Tundra mire</td>
<td>68°21'N 19°05'E</td>
<td>Granhall and Selander, 1973; Basilier and Granhall, 1978</td>
<td>+</td>
<td>+</td>
<td>+96</td>
<td>+ MT 75</td>
<td>+</td>
</tr>
<tr>
<td>Boreal-arctic forest</td>
<td>60°21'N 106°54'W</td>
<td>Garrity and Kershaw, 1978</td>
<td>+</td>
<td>+</td>
<td>+34</td>
<td>+ T 84–89</td>
<td>+</td>
</tr>
<tr>
<td>Coastal tundra</td>
<td>71°17'N 156°45'W</td>
<td>Gersper et al., 1980</td>
<td>+</td>
<td>+</td>
<td>+96</td>
<td>+ MT 75</td>
<td>+</td>
</tr>
<tr>
<td>High arctic lowland</td>
<td>78°53'N 75°55'W</td>
<td>Henry and Svoboda, 1986</td>
<td>+</td>
<td>+</td>
<td>+34</td>
<td>+ T 84–89</td>
<td>+</td>
</tr>
<tr>
<td>High arctic lowland</td>
<td>78°53'N 75°55'W</td>
<td>Chapin et al., 1991</td>
<td>+</td>
<td>OT 15–25</td>
<td>+5</td>
<td>+ T 80–90</td>
<td>+</td>
</tr>
<tr>
<td>Tundra mire,</td>
<td>69°45'N, 27°01'E</td>
<td>Alexander and Schell, 1973; Schell and Alexander, 1973;</td>
<td>+</td>
<td>+</td>
<td>+23</td>
<td>+ MT 17,</td>
<td>+</td>
</tr>
<tr>
<td>Alpine heath</td>
<td>71°20'N 156°38'W</td>
<td>Alexander et al., 1978</td>
<td>+</td>
<td>+</td>
<td>+23</td>
<td>+ MT 17,</td>
<td>+</td>
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<tr>
<td>High arctic lowland</td>
<td>75°33'N 84°40'W</td>
<td>Lennihan et al., 1994</td>
<td>+</td>
<td>+</td>
<td>+23</td>
<td>+ MT 17,</td>
<td>+</td>
</tr>
<tr>
<td>Low arctic alpine</td>
<td>68°08'N 151°45'W</td>
<td>Nash and Olafsen, 1995</td>
<td>+</td>
<td>+</td>
<td>+23</td>
<td>+ MT 17,</td>
<td>+</td>
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<tr>
<td>Polar desert</td>
<td>78°53'N 75°55'W</td>
<td>Liengen and Olsen, 1997a; Liengen, 1999a</td>
<td>+</td>
<td>+</td>
<td>+23</td>
<td>+ MT 17,</td>
<td>+</td>
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<tr>
<td>Boreal-arctic forest</td>
<td>68°35'N 18°82'E</td>
<td>Solheim et al., 2002</td>
<td>+</td>
<td>+</td>
<td>+20</td>
<td>+ MT 17,</td>
<td>+</td>
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<tr>
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<td>78°47'N 15°19'E</td>
<td>Ziekel et al., 2002</td>
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<td>+</td>
<td>+20</td>
<td>+ MT 17,</td>
<td>+</td>
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<td>Tussock tundra</td>
<td>68°37°N 14°19'W</td>
<td>Hobar et al., 2006</td>
<td>+</td>
<td>+</td>
<td>+20</td>
<td>+ MT 17,</td>
<td>+</td>
</tr>
<tr>
<td>Low arctic alpine</td>
<td>61°10'N 130°26'W</td>
<td>Marsh et al., 2006</td>
<td>+</td>
<td>+</td>
<td>+20</td>
<td>+ MT 17,</td>
<td>+</td>
</tr>
<tr>
<td>Tundra mire</td>
<td>68°19°N 18°51'E</td>
<td>Sorensen et al., 2006</td>
<td>+</td>
<td>+</td>
<td>+20</td>
<td>+ MT 17,</td>
<td>+</td>
</tr>
<tr>
<td>Polar desert</td>
<td>79°10°N 79°45'W</td>
<td>Breen and Lesvesque, 2008</td>
<td>+</td>
<td>+</td>
<td>+20</td>
<td>+ MT 17,</td>
<td>+</td>
</tr>
</tbody>
</table>

**T** – Topographic gradient relating to larger landscape features such as catenas, eskers, ridges etc. **MT** – Microtopographic gradient relating to smaller landscape features such as frost boils, hummock-hollow complexes and polygons. **OT** – Optimal temperature leading to the highest rate of N₂-fixation compared with other temperatures (°C). **MN** – Mineralizable Nitrogen, **TN** – Total Nitrogen, **TC** – Total Carbon, **OC** – Organic Carbon.
Topography is the primary determinant of soil moisture patterns across arctic landscapes and plays a major role in determining the distribution of vegetation types and plant community succession (Chapin et al., 1991; Walker, 2000). In addition, variation in plant biomass, rates of primary productivity, soil organic matter (SOM) quantity and quality, nutrient status and soil chemistry are all tightly linked to topography (Shaver and Chapin, 1980; Walker, 1985; Giblin et al., 1991; Nadelhoffer et al., 1991; Bliss and Matveyeva, 1992; Forbes et al., 2001; Paré and Bedard-Haughn, 2012). Microtopographical features within arctic landscapes are often related to periglacial landforms such as hummock-hollow complexes, frost boils and polygonal ground. Corresponding topographical gradients of soil moisture, temperature and nutrients tend to occur at the landscape and larger spatial scales across the Arctic (Mueller et al., 1999; Kaiser et al., 2005; Stewart et al., 2011c; Fig. 3; Table 2).

Moisture is the primary factor controlling N2-fixation across various arctic ecosystems (Alexander, 1974; Alexander et al., 1978; Davey, 1983; Chapin and Bledsoe, 1992; Line, 1992; Zelke et al., 2002, 2005; Convey and Smith, 2006; Stewart et al., 2011b). Higher precipitation inputs due to climate change may account for 20% of the increase in N2-fixation rates in arctic environments (Chapin and Bledsoe, 1992; Table 1). Seasonally, overall N2-fixation rates are lower during summers with low rainfall (Gersper et al., 1980). Correlation of N2-fixation rates with soil moisture or water content of lichen thalli or moss tissues provide evidence of the important direct effect of moisture on activities of free-living and symbiotic cyanobacteria. Moisture also indirectly enhances N2-fixation by stimulating net primary production, thereby increasing SOM inputs and by transporting dissolved organic carbon and nutrients downslope (Wierenga et al., 1987; Hartley and Schlesinger, 2002). Rapid changes in moisture regime can also result in the mobilization of previously stored sugars and N-amino acids in mosses and lichens (Wilson and Coxson, 1999).

The distribution of vegetation types and their associative N2-fixing communities are strongly influenced by topographical moisture gradients. Lichens tend to be found on higher soil positions (crests and beach ridges) and can dominate vegetation communities under harsh and exposed conditions (Figs. 1 and 3). Higher abundance of lichens at higher topographical positions can lead to increased rates of N2-fixation under these drier conditions (Hobara et al., 2006; Table 1). However under moist conditions, higher rates of N2-fixation are generally associated with lower positions within arctic landscapes with an increase in N2-fixation rates observed at lower topographical and microtopographical positions (Table 1). Bryophytes and dwarf shrubs preferentially occupy these lower slope positions where there is greater moisture availability (Schell and Alexander, 1973; Tenhunen et al., 1992; Hobara et al., 2006; Fig. 3), where lichens are excluded by competitive displacement (Joly et al., 2009), and by their inability to tolerate prolonged hydration episodes (Moser and Nash, 1978; Fig. 2). Both the proximity of permafrost to the soil surface, and moisture retention by bryophytes, help to create a moist environment in these low-lying areas, which is likely crucial in maintaining high rates of N2-fixation. In addition, nutrient transport at the microtopographical scale from the higher mounded areas may increase dissolved organic and inorganic nutrients, such as C and P in hollows, which in turn may promote N2-fixation in these hollows (Fig. 3). Furthermore, this effect may be just as important at the landscape scale since there is great potential for movement of dust and surface run-off from higher to lower elevation ecosystems.

The estimates of optimum temperature for N2-fixation in the Arctic vary from 15 to 30 °C (Alexander, 1974; Kallio and Kallio, 1997a; Zelke et al., 2002; Sorensen et al., 2006) (Table 1). Furthermore, our analysis suggests that topography and microtopography play critical roles through their influence on abiotic and biotic factors that in turn affect both N2-fixation and N biogeochemical cycling in northern landscapes (Table 1; Fig. 3).
Table 2
Factors influencing soil characteristics, mineralization and nitrification and denitrification rates in arctic ecosystems. For each study an increase (+) or decrease (−) at a lower topographical position for soil characteristics and/or N transformations are given. Percentages of increase or decrease are given for studies where values or means were given. Ranges of percentages were calculated by comparing values or means with the most extreme to least extreme difference. Variables that appear in bold italics were not measured in relation to topography but refer only to the given N transformation.

<table>
<thead>
<tr>
<th>Ecosystem type</th>
<th>Location</th>
<th>Study</th>
<th>Lower topographic or microtopographical position</th>
<th>Soil moisture (%)</th>
<th>Soil temperature (%)</th>
<th>Soil organic matter (%)</th>
<th>C, N, C:N (%)</th>
<th>Mineralization/Immobilization (%)</th>
<th>Nitrification (%)</th>
<th>N2O flux (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal tundra</td>
<td>71°17’N 156°45’W</td>
<td>Gersper et al., 1980</td>
<td>+40–43, +5–19</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>−NN 37</td>
<td>+C</td>
</tr>
<tr>
<td>Willow-herb hummock and wet sedge tundra</td>
<td>75°33’N 84°40’W</td>
<td>Chapin, 1996</td>
<td>+52</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>−NN 84</td>
<td>−pH, −SM, −NO3</td>
</tr>
<tr>
<td>Low shrub-moss-lichen tundra</td>
<td>66°23’n 65°28’W</td>
<td>Mueller et al., 1999</td>
<td>+~45</td>
<td>+HD ~70</td>
<td>+C ~30, +N ~30</td>
<td></td>
<td></td>
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<tr>
<td>Tussock tundra</td>
<td>68°38’N 149°38’W</td>
<td>Schimel et al., 2004</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+NM 37, −1</td>
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<tr>
<td>Frost-boil tundra</td>
<td>69°43’n 74°39’E</td>
<td>Kaiser et al., 2005</td>
<td>+~65</td>
<td>−~20</td>
<td>+HD ~93</td>
<td>+C 85, +MBN ~75, +DON 45, +NH4+58, +N ~55–85, +C:N ~100</td>
<td></td>
<td></td>
<td>+NM 35, −GI 88</td>
<td></td>
</tr>
<tr>
<td>Tussock tundra</td>
<td>68°37’n 149°1’W</td>
<td>Hobarra et al., 2006</td>
<td>+40–75</td>
<td>+30–97</td>
<td>+NH4+80–96, +NO3−80–82</td>
<td></td>
<td></td>
<td>+64–87</td>
<td>+NH4+, −SM</td>
<td></td>
</tr>
<tr>
<td>High arctic lowland</td>
<td>75°40’n 84°35’W</td>
<td>Ma et al., 2007</td>
<td>+40–75</td>
<td>+30–97</td>
<td>+NH4+80–96, +NO3−80–82</td>
<td></td>
<td></td>
<td>+64–87</td>
<td>+NH4+, −SM</td>
<td></td>
</tr>
<tr>
<td>Tundra to polar desert</td>
<td>69°13’n 148°84’W</td>
<td>Michaelson et al., 2008</td>
<td>+5%</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+C 80, +N 36, +C:N 20</td>
<td></td>
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<tr>
<td>Low arctic tundra</td>
<td>78°79’n, 103°55’W</td>
<td>Buckeridge et al., 2010b; Buckeridge et al., 2010a</td>
<td>+5%</td>
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<tr>
<td>Low arctic tundra</td>
<td>64°50’n 111°38’W</td>
<td>Chu and Grogan, 2010</td>
<td>+52</td>
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<tr>
<td>Low arctic tundra</td>
<td>64°50’n 111°38’W</td>
<td>Stewart et al., 2011b</td>
<td>+52</td>
<td></td>
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</tr>
<tr>
<td>Boreal-arctic forest, Lichen-bryophyte-grummnoid tundra</td>
<td>58°45’n 93°51’W</td>
<td>Paré, 2011; Paré and Bedard-Haughn, 2012</td>
<td>+16–90</td>
<td>−13–63</td>
<td>+C 41–73, +DON 60–72, +NH4+28, +NO3−7, +N ~18–58, +C:N 22</td>
<td></td>
<td></td>
<td>+GM 51–79</td>
<td>+C, +N, +NH4+</td>
<td></td>
</tr>
<tr>
<td>High arctic lowland</td>
<td>68°31’n 111°10’W</td>
<td>Banerjee and Siciliano, 2012a</td>
<td>+52</td>
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</table>

1975; Chapin and Bledsoe, 1992; Hobara et al., 2006; Table 1), which is well above the average surface temperature of 7 °C. Most N_2 fixers appear to reach optimal rates of N_2-fixation at approximately 21 °C and show a rapid increase in rates at temperatures above 10 °C, whereas N_2-fixation rates at or below 0 °C are low but detectable (0.33–1 μmol N m⁻² h⁻¹ based on a 3:1 C₂H₂:N₂ conversion ratio) (Davey and Marchant, 1983; Chapin et al., 1991; Chapin and Bledsoe, 1992; Lennihan et al., 1994; Ziekel et al., 2002; Hobara et al., 2006). Detectable nitrogenase activity under low temperature conditions is coupled with the ability of cyanobacteria to survive long-term freezing at −20 °C (Davey, 1983; Liengen, 1999a) and photosynthesis by Nostoc commune can continue at very low temperatures (−4 °C), which enables nitrogenase activity to proceed until it is inhibited by complete cellular freezing (Davey, 1983). Coxson and Kershaw (1983) found no winter inactivation of the nitrogenase enzyme and suggest that the elimination of nitrogenase activity in N. commune colonies under snowpack is likely due to depletion of carbohydrate pools supplying energy to the reaction in the dark, rather than direct inactivation of nitrogenase activity by freezing temperatures. Thus, despite an adaptation to cold temperatures, temperature is still an important limiting factor for N_2-fixing organisms in the Arctic (Chapin et al., 1991).

Relative to moisture and temperature, light is likely the least limiting factor in polar environments. Some studies found N_2-fixation to be light-dependent (Granhall and Lid-Torsvik, 1975; Alexander et al., 1978) while others found light dependence as photosynthetic rates tend to saturate at low light levels (<500 μmol m⁻² s⁻¹) (Coxson and Kershaw, 1983; Chapin and Bledsoe, 1992; Ziekel et al., 2002) (Table 1). The ability of cyanobacteria to use stored energy for N_2-fixation combined with continuous or near continuous daylight over the growing season, as well as, an undeveloped plant canopy, limits the potential for light to act as a controlling factor on N_2-fixation rates in the Arctic (Chapin and Bledsoe, 1992). In addition, although increasing light intensity may be positively correlated with increased N_2-fixation rates, light intensity is often coupled with surface temperature suggesting that surface soil temperatures are likely the ultimate driving factor (Sorensen et al., 2006). Numerous studies have documented that light availability can modify boundary layer microclimate, especially surface temperatures, with arctic soil surface lichen thalli or BSCs exhibiting temperature gradients of up to 20 °C over ambient air temperatures under full sun conditions (Kershaw, 1977; Molgaard, 1982; Kappen, 2000; Stewart et al., 2011a). Despite the influence of solar inputs on surface temperatures, climate changes that result in more cloud cover may have little direct effect on N_2-fixation because most cyanobacteria achieve light saturation at low light levels and corresponding increases in precipitation are expected to increase N_2-fixation (Ziekel et al., 2002).

There are several challenges associated with in-situ measurement of biological N_2-fixation in harsh arctic environments with short growing seasons. Optimal rather than in-situ rates are often reported, and therefore do not reflect the importance of environmental conditions limiting N_2-fixation rates within a given landscape. In addition, almost all N_2-fixation studies in northern environments have used Acetylene Reduction Assays (ARAs). The conversion factor between ARA rates and N_2-fixation rates has been a long-standing challenge when using ARA rates to estimate N input via N_2-fixation. The theoretical ratio of acetylene reduced:nitrogen reduced is 3:1, however in practice the ratio differs significantly (Gunther, 1989; Stewart et al., 2011a). Differences between the theoretical and actual conversion ratio are due to the higher solubility of acetylene and differences in the electron-transfer efficiencies between N₂ and acetylene (Smith, 1982). In addition, conversion ratios vary between different N_2-fixing associations and are likely not consistent over different environmental conditions (Millbank, 1981; Gunther, 1989). Conversion ratios from various studies range as widely as <0.01–25 (Millbank and Olsen, 1986; Liengen, 1999b; Hobara et al., 2006) and the use of a single conversion ratio for all N_2-fixing associations under all environmental conditions impacts the accuracy of N input estimates from biological N_2-fixation.

5. Biological N₂-fixation as a source of soil and plant N

In polar deserts total soil N is often very low (0.04%), however, soil N can increase by more than twice where BSCs are present (Gold and Bliss, 1995). N_2-fixation in such environments may be high enough to meet the entire N needs of the system and promote growth in low biomass polar deserts (Dickson, 2000). Increased BSC development is correlated with increased vascular plant abundance (Anderson and Bliss, 1998) and increased soil nutrient availability, SOM and moisture retention (Gold and Bliss, 1995; Gold, 1998; Bliss and Gold, 1999; Dickson, 2000) (Table 1). Observation of higher productivity in arctic grasses with epiphytic nitrogen fixing cyanobacteria indicates an effective transfer of fixed N to the plant community (Solheim et al., 1996). In our extensive review of the literature, we found there was higher total N, mineralizable N, total carbon and organic carbon in soils where higher rates of N_2-fixation were detected (Table 1), altogether supporting the idea that biological N_2-fixers act as important point sources of N and C in arctic ecosystems.

The role that different N_2-fixing associations play in altering nutrient availability and the extent and importance of organic N versus N mineralization and inorganic N remains understudied or controversial (Belnap, 2001; Johnson et al., 2005; Knowles et al., 2006; Lagerström et al., 2007). Organic N compounds (e.g. peptides, amino acids and amides) often comprise a large portion of the total dissolved N released from N_2-fixing organisms (Alexander and Schell, 1973; Johnson et al., 2005; Fig. 1: pathway c). Inorganic N supplied to plants by mineralization of this organic N (Fig. 1: pathway d) may not be sufficient to meet the annual requirement of N by many tundra species and thus organic N may act as an important direct source of N to plants in the Arctic (Kielland, 1994; Jonasson et al., 1999a,b; Schimel and Bennett, 2004b) (Fig. 1: pathway e). Nitrogen mineralization was once considered to be the bottle-neck in the N cycle of arctic systems (Nadelhoffer et al., 1991; Kielland, 1994), but now it is quite clear that many arctic plant species may be able to short-circuit the mineralization step by directly acquiring dissolved organic N (Chapin et al., 1993; McKane et al., 1997; Schimel and Bennett, 2004b; Fig. 3). Mineralization is low in tundra soils and concentrations of inorganic N are low, however soils have large stocks of both structural and soluble organic N (Kielland, 1994, 1995; Paré and Bedard-Haughn, 2013). Root uptake of amino acids in intact form has been demonstrated and may account for 10–82% of total plant N uptake (Kielland, 1994; Jones et al., 2005). In addition, the shallow rooting system of arctic plants, primarily due to thin active layers, may allow plants to directly access nutrients released from BSCs (Breen and Levesque, 2008).

N input via biological N₂-fixation is often very low in comparison to internal recycling of N from litter and SOM. However, the rate of N mineralization, not just the N pool size may play an important role in N uptake by plants (Schimel and Bennett, 2004; Buckeridge et al., 2010a). Some tundra warming experiments have found that increased aboveground growth, particularly of shrubs, is due to faster soil N cycling (Chapin et al., 1995; Walker et al., 2006; Buckeridge et al., 2010b). Thus, it may be that cyanobacteria are contributing to a fast cycling pool of soil N which has been found to be critical for plant growth.
Interactions between the soil microbial community and plants are a major factor controlling N cycling within a given ecosystem (Kaye and Hart, 1997; Hawkes, 2003). While rates of N input via N₂-fixation undoubtedly play a role in N available for plant uptake, soil microbial communities are the dominant force behind the N cycling in soil and may play the most vital role in plant N availability (Knops et al., 2002). The BSCs not only contain associative N₂-fixing organisms but also heterotrophs which, when N is scarce, will compete with vascular plants for this N (Fig. 1: pathway b). Thus, the relative abundance of microbes that can and cannot fix N₂ (e.g. cyanobacteria and heterotrophs respectively) will determine whether a BSC acts as a net N source or sink (Hawkes, 2003). For example, a lack of N output from BSC suggests that associated microbes are assimilating leaked inorganic and organic N compounds within the BSC (Johnson et al., 2005). In addition, lichens, bryophytes and BSCs also act as filters through which exogenous N must pass. Mat-forming lichens in polar ecosystems can retain >80% of NH₄⁺ and NO₃⁻ deposited in summer rainfall (Crittenden, 1983, 1996) and mat-forming mosses can sequester nutrients and carbon at low concentrations from atmospheric sources (Fig. 1: pathway b), which are later released at higher concentrations during rewetting events (Wilson and Coxson, 1999). During the initial (N) phase of hikoku when cell wall integrity has not been fully restored, previously sequestered nutrients can be released to through flow solutions, providing easily assimilated N- and C-rich substrates for underlying soil microbial communities. Thus, various N₂-fixing associations can act as both sources and sinks of N for the remainder of the terrestrial ecosystem.

Topography in arctic landscapes is the key landscape-level driver of soil N availability to plants in the Arctic. Topographic patterns are known to determine both temperature and moisture gradients, which are important driving factor in controlling nutrient turnover (Mueller et al., 1999; Walker et al., 2004; Biasi et al., 2005). Nitrogen, C and organic matter contents in soil vary systematically down hillslopes or catenas (Miller, 1982; Schimel et al., 1985; Walker et al., 1989; Burke, 1989; Giblin et al., 1991; Paré and Bedard-Haughn, 2012). Increased N and P availability and primary productivity are often found in downslope areas or in topographic depressions. Higher N, available P and potassium pools, as well as faster rates of N mineralization and decomposition (i.e. CO₂ emissions) occur in inter-hummock areas or trough areas associated with frost boils and polygons (Mueller et al., 1999; Walker et al., 2004; Biasi et al., 2005; Nobrega and Grogan, 2008; Paré and Bedard-Haughn, 2012).

Redistribution of water-soluble soil nutrients from higher to lower lying topographic positions with water, wind, and snow (Kummerow et al., 1987; Fahnstock et al., 2000) creates fertile conditions for plant growth in lower-slope positions (Schimel et al., 1985, 2004; Christensen et al., 1999; Paré and Bedard-Haughn, 2012). Low temperature, as well as, high soil moisture may limit microbial decomposition of SOM and hence may promote the accumulation of labile SOM in low-lying areas (Hobbie et al., 2000; Weintraub and Schimel, 2005; Paré, 2011). SOM quantity and characteristics alter N mineralization rates (Nadelhoffer et al., 1991; Hobbie, 1995, 1996; Sjögersten and Wookey, 2005; Paré and Bedard-Haughn, 2012). Therefore, similar to temperate ecosystems (Hart et al., 1994), it appears that arctic soil N cycling is influenced by the type and characteristics of SOM, which is in turn, dictated by topography. Increases in snow depth, often in lower lying areas, consistently result in increases in winter soil temperature (Walker et al., 1999; Schimel et al., 2004; Buckeridge and Grogan, 2008) and may increase winter soil microbial activity (Nobrega and Grogan, 2007; Grogan, 2012). Accordingly, in our review of arctic studies relating abiotic controls to soil N transformation processes along hillslope or microtopographical positions, there were consistently higher N, C, SOM and mineralization rates in lower topographical or microtopographical positions compared to higher positions (Table 2).

6. Gaseous N loss from arctic soils

Approximately 70% of global N₂O emissions are due to microbial nitrification and denitrification (Syakila and Kroeze, 2011; Braker and Conrad, 2011). There are many pathways by which N can be lost from arctic ecosystems and a discussion of all microbial metabolic pathways that form or consume N₂O and N₂ exceeds the scope of this review. Here we focus upon the processes of microbial nitrification and denitrification. For a comprehensive description of all pathways currently understood to play a role in N₂O and N₂ production and consumption see Butterbach-Bahl et al. (2013). Losses of N occur in both inorganic and dissolved or suspended organic forms and via both surface and subsurface flow (Gersper et al., 1980). Since nitrate and nitrite are not involved in exchange processes with exchange sites (i.e. clay, metal oxides, SOM), they are more mobile than ammonium and more prone to leaching or loss via surface runoff (Gersper et al., 1980). Not only is nitrate more easily leached from soils than ammonium, it can also be lost from the ecosystem via denitrification (Nadelhoffer et al., 1991). N₂-fixation is not only necessary for new N input in arctic ecosystems, but may also play an important role in replacing N accumulation in permafrost. Losses by leaching and runoff, as well as losses through denitrification, since conditions that tend to promote N₂-fixation may also promote denitrification (Chapin, 1996; Sørensen et al., 2006). Spatial correlations between N₂-fixation and denitrification rates have been recognized globally (Cleveland et al., 1999; Seitzinger et al., 2006; Reed et al., 2011), however relatively few studies have examined these linkages in arctic ecosystems.

Several studies from temperate ecosystems demonstrate a positive effect of soil moisture on N₂O emissions (Pennock et al., 1992; Van Kessel et al., 1993; Yates et al., 2006; Smith et al., 2008; Rochette et al., 2010) and there are a growing number of studies from arctic ecosystems that similarly suggest that increasing soil moisture may increase N₂O emissions (Ma et al., 2007; Elberling et al., 2010; Banerjee and Siciliano, 2012b; Brumell et al., 2012) (Table 2). As previously discussed, soil moisture gradients in arctic landscapes are often controlled by topographic gradients; therefore, topography is a key factor for N₂O emissions. Paré and Bedard-Haughn (2012) did not find significant differences in N₂O emissions with topography, which was likely due to the extremely low levels of emissions detected across the study sites. However, Ma et al. (2007) found that cumulative N₂O emissions in a high arctic lowland ecosystem were closely associated with the hydrological gradient across the landscape. The lowest emissions occurred on raised beach crests with increasing emissions from lower foreslope to wet sedge meadows. Reduction of nitrate to nitrite measured in tundra coastal soils at Barrow Alaska showed higher rates in polygon troughs compared with high-centred polygons and in general higher N₂O emissions were measured in low-lying wet sedge meadows (Gersper et al., 1980). Currently, there are only a few arctic studies examining N₂O flux across topographical gradients, however, in our review the majority of studies found significantly higher N₂O emissions occur in lower slope positions with higher soil moisture (Table 2; Fig. 3).

Higher quantities of easily decomposable SOM, as well as, inorganic N can increase N₂O emissions in arctic ecosystems. Labile C can affect soil denitrification by providing an energy source for denitrifying soil microbes in the production of N₂O and local anoxia can induce denitrification by forcing heterotrophs to switch from oxic to anoxic metabolism (Garcia-Montiel et al., 2003; Paré, 2011). While easily decomposable OM stimulates denitrification in
temperate soils, very few studies have examined the relationship between SOM and denitrification in arctic soils (Gersper et al., 1980; Paré, 2011). The addition of inorganic N stimulates denitrification (Chapin, 1996; Christensen et al., 1999; Sorensen et al., 2006; Ma et al., 2007; Siciliano et al., 2009; Buckeridge et al., 2010a). While environmental conditions in the Arctic may at times be favourable for N₂O emissions, particularly in areas with high soil moisture and SOM, low soil inorganic N in arctic soils appears to limit N₂O emissions. For example, chronic high level NH₄–N₂O fertilization elevated early springtime net N₂O efflux from mesic birch hummock tundra by 1–2 orders of magnitude compared to the almost negligible levels in control plots, indicating that the microbial community responsible for this process was present but strongly limited in activity by the scarcity of substrate (Buckeridge et al., 2010a) (Fig. 1, pathway f). Denitrification is typically detected only when soils were fertilized with inorganic N (Buckeridge et al., 2010a) and not with organic N (Christensen et al., 1999). All of the studies we reviewed observed higher N₂O emissions with higher soil NO₃, NH₄ or total N (Table 2). Higher inorganic N availability in soils in lower lying areas may partly account for the higher rates of N₂O emissions detected there.

Previous studies from across the Arctic show very low N₂O emissions from some ecosystems with the exception of arctic wetlands (Christensen et al., 1999; Rodionow et al., 2006; Sorensen et al., 2006; Churchill, 2007; Repo et al., 2009; Elberling et al., 2010; Paré and Bedard-Haughn, 2012). In fact, many arctic soils may act as N₂O sinks (Buckeridge et al., 2010a Paré and Bedard-Haughn, 2012; Stewart et al., 2012b). However, relatively few studies report net negative N₂O flux, especially under dry conditions like those found in polar deserts (Donoso et al., 1993; Yamulki et al., 1995; Klemmedtsson et al., 1997; Verchot et al., 1999; Flechard et al., 2005; Goldberg and Gebauer, 2009; Stewart et al., 2012b) and the mechanisms associated with these N₂O sinks are poorly understood. Net negative N₂O flux is not only dependent on the potential for N₂O reduction to N₂, but factors such as the diffusivity of N₂O within the soil profile and the dissolution of N₂O into soil water (Ryden, 1981; Chapuis-Lardy et al., 2007). Water-dissolved N₂O can be transported with drainage to other locations and generate N₂O emissions elsewhere, confounding the relationship between controlling factors in the soil and surface N₂O flux (Heincke and Kaupenjohann, 1999; Well et al., 2001; Chapuis-Lardy et al., 2007). In addition, cryoturbation may act to redistribute SOM and nutrients influencing active populations of microorganisms further contributing to variation in N₂O emissions (Repo et al., 2009; Brumell et al., 2012).

6.1. Denitrification and nitrifier denitrification in soils

Most studies clearly indicate that higher N₂O emissions are detected in low-lying areas and this is often attributed to higher rates of denitrification. Production of N₂O in soils can arise from different assimilative or dissipative pathways (Stein, 2011). There are two main pathways by which N₂O and N₂ are formed in arctic ecosystems: denitrification and nitrifier denitrification (Fig. 1: pathway g). Denitrification is the respiratory reduction of NO₃ and NO₂ to N₂O and N₂ (Tiedje, 1984). Net N₂O consumption during denitrification by denitrifying bacteria can occur, reducing N₂O to N₂ (Chapuis-Lardy et al., 2007). In addition, bacterial nitrifiers also possess the ability to denitrify, however, it is not yet known how common the ability to reduce N₂O to N₂ is in nitrifiers (Chapuis-Lardy et al., 2007). The relative importance of these two pathways is also strongly influenced by a number of edaphic factors and their influence on denitrifying bacteria and fungi and nitrifying bacteria respectively. Soil moisture and its direct influence on O₂ availability and N substrate availability are the main controlling factors. Nitrification is an aerobic process, however nitrifier denitrification occurs when O₂ availability is limited and nitrifiers use nitrite as an electron acceptor producing NO and N₂O (Bollman and Conrad, 1998; Ma et al., 2007; Stewart et al., 2012a). Nitrification tends to occur at water contents up to 60% Water Filled Pore Space (WFPS) while denitrification becomes the dominant process when WFPS exceeds 60% (Lemke et al., 1998; Davidson and Verchot, 2000; Ma et al., 2007). While bacterial denitrification is the dominant mechanism producing N₂O in temperate systems (Dalal and Allen, 2008), recent studies suggest that N₂O released in arctic environments may be primarily from the activity of prokaryotic nitrification–denitrification and fungal denitrification pathways (Ma et al., 2007, 2008; Siciliano et al., 2009; Lamb et al., 2011). Nitrous oxide release arises from nitrification as either a reduction of NO produced during ammonia oxidation or directly from coupled nitrification-denitrification. The release of N₂O from these processes would be less than that from denitrification under ideal conditions in which denitrifiers did not compete for NO₃ but under typical soil conditions, competition for NO₃ severely limits denitrification compared to nitrification activity (Siciliano et al., 2009). Higher rates of N₂O emissions generally occur at lower topographical or microtopographical positions and these emissions may be driven by the uncoupled denitrification pathways. Under typical soil conditions of low-lying areas may allow for nitrous oxide reductase to always be fully active, and therefore denitrifiers likely contribute little to N₂O flux. In contrast, under the moisture-limited conditions that occur in higher topographical positions, N₂O reductase is not fully induced and therefore denitrifier activity is likely the main determinant of N₂O flux (Stewart et al., 2012a).

The influence of hydrological gradients associated with topography on N₂O emissions may also be attributed to moisture-regulated patterns of N mineralization that determine N availability. Paré and Bedard-Haughn (2012) found a weak but significant positive correlation between N₂O emissions and soil gross N mineralization, suggesting that nitrifier denitrification is an active N pathway under arctic soil conditions (Table 2; Fig. 1, pathway f). Ma et al. (2007) found N₂O emissions in a high arctic wet sedge meadow decreased with decreasing soil NH₄ and that NH₄ rather than NO₃ correlated with cumulative N₂O flux. Our review indicates that N mineralization and N₂O fluxes tend to be largest in relatively low-lying areas in arctic landscapes.

While mineralization rates and NH₄ availability likely play an important role in N₂O flux via the nitrifier denitrification pathway, there is also evidence that NO₃ and nitrification contribute to N₂O emissions (Table 2). For example, the soil N cycle was closely linked to N₂O emissions via nitrification in a high arctic wet sedge meadow but via NO₃→N in a high arctic Dryas spp. dominated heath ecosystem (Stewart et al., 2012a). The direct influence of inorganic N and in particular NO₃−N on N₂O emissions likely indicates a nitrification-coupled denitrification pathway (i.e. N₂O produced from denitrifiers by reduction of NO₃→produced from nitrification) as the primary source of N₂O emissions (Ma et al., 2008; Kool et al., 2011; Stewart et al., 2012a). Increased N cycling rates promote nitrification, which either directly releases N₂O (Ma et al., 2007, 2008) or in turn stimulates denitrification which also releases N₂O (Nadelhoffer et al., 1992; Paul and Clark, 1996; Walker et al., 2008; Stewart et al., 2012a).

In our review of nitrification studies across the Arctic (Table 2), we found some reports of substantial net nitrification rates (Gersper et al., 1980; Giblin et al., 1991; Nadelhoffer et al., 1991; Bañé and Siciliano, 2012a) while others reported low or negligible nitrification rates (Rosswall and Granhall, 1980; Van Cleve and Alexander, 1981), low temperature and anoxic conditions are all explanatory factors for low nitrification (Nadelhoffer et al., 1992;
In addition, temperature may be a major limiting factor for nitrification with detection of nitrification only occasionally occurring below 5 °C (Gersper et al., 1980). Some studies found nitrification to be primarily controlled by a soil moisture gradient associated with topography (Giblin et al., 1991; Chapin, 1996) (Table 2) with nitrification inhibited in wet footslope ecosystems. While some arctic studies we reviewed had higher net nitrification or nitrification potential in lower topographical positions, the majority reported higher soil moisture, lower temperature and lower net nitrification in lower topographical positions (Table 2). Overall, it is clear that soil moisture, O2 availability and N substrate are key factors influencing overall N2O emissions and that there are similarities in the enzyme systems of nitrifiers and denitrifiers, but nevertheless the biochemical processes of nitrifier denitrification and denitrification may not be regulated in a similar manner with respect to moisture content and related aerobicity (Kool et al., 2011). N2O emissions may increase or decrease with increasing WFPS, depending on the group of organisms and the biochemical pathways that are present and active (Corre et al., 1996; Ma et al., 2007; Bremer et al., 2009; Brummell et al., 2012). For example, increased aerobic conditions, increased N mineralization, lead to an increase in nitrification which releases N2O whereas increasingly anaerobic conditions increase denitrification activity which releases N2O. Further studies are required to determine the relative importance of nitrifier denitrification and denitrification in arctic ecosystems and to identify the key driving factors for these two pathways. Recent advances in stable isotope techniques, including both enrichments and natural abundance (18O, 15N) may offer a means to examine the contribution of different microbial processes (Baggs, 2008). N2O produced during nitrification is more depleted in 15N and 18O relative to N2O produced during denitrification, however isotopic techniques have not yet been applied to distinguish between all known microbial sources of N2O simultaneously (Butterbach-Bahl et al., 2013).

Furthermore, our understanding of the ability of arctic soils to sustain nitrifier and denitrifier communities to an extent that measurable gaseous N loss occurs requires further investigation. Recent reports of N2O production by oceanic ammonia-oxidizing archaea (AOA) (Santoro et al., 2011) indicate that while AOA can contribute to N2O production this is likely arising due to hydroxylamine production (Vajrala et al., 2013). However, gross arctic nitrification rates across 11 sites were closely linked to different clades of AOA (Alves et al., 2013) and suggest that AOA may be a dominant group in the arctic environment. At temperate and tropical sites, preliminary results (Adair et al., 2013) are suggesting that AOA dominance may be linked to the isotopic signature of soil N implying the importance of AOA in gaseous N cycling in soil ecosystems. In summary, our current understanding is that AOA can be involved in gaseous N release but that the N2O release rates of AOA are very low (Santoro et al., 2011) and do not occur under anaerobic conditions. In contrast, AOB (ammonia-oxidizing bacteria) produce N2O at higher rates and can do so under anaerobic conditions via denitrification coupling. However, it is still unclear whether nitrification is driven by AOBs in arctic environments and also unclear whether the mechanisms leading to N2O production in AOBs are the same as those leading to N2O production in AOA.

7. N2 emissions

There are relatively few studies that provide measurement of N2 emissions and to our knowledge only one study that specifically addresses N2 emissions within an arctic terrestrial environment (Palmer et al., 2012). In general, this scarcity is primarily due to the methodological problems of measuring N2 production via denitrification and disentangling N2O production processes at a field scale (Groffman et al., 2006; Butterbach-Bahl et al., 2013). Acetylene inhibition methods have been used to quantify N2O + N2 production by inhibiting N2O reduction to N2 via denitrification (Klemmedtsson et al., 1988; Kitzler et al., 2006). However, under aerobic conditions the acetylene inhibition method is known to produce underestimation of N2 production by denitrification and N2O/(N2O + N2) ratios obtained are systematically higher compared with those determined by the gas-flow helium incubation method or isotopic labelling (i.e. the determination of labelled N2 following the application of 15N-labelled substrates) (Bollmann and Conrad, 1997; Groffman et al., 2006; Yu et al., 2010; Butterbach-Bahl et al., 2013).

Gas-flow helium and isotopic labelling also have limitations due to severe perturbation of the soil’s PO2 when removing N2, and a fertilization effect respectively. Butterbach-Bahl et al. (2013) summarized all available datasets where N2 emissions have been measured by the latter two approaches. A few studies have applied the acetylene inhibition method in terrestrial arctic environments and these studies have focused upon determination of N2O from nitrification versus denitrification rather than as a means to effectively quantify N2 emissions (Chapin, 1996; Ma et al., 2007; Palmer et al., 2012). Palmer et al., 2012 compared cryoturbated and unturbated peat soils and found cryoturbation favours the production of N2 whereas, in unturbated peat, N2O was the main end product of denitrification. However, in cryoturbated peat soils, N2O that was initially produced from internal-N sources was consumed, indicating the capability of peat soil denitrifiers for complete denitrification to N2 under acidic conditions. Ratios of N2O to total N gases were below 40% at low nitrate and nitrite concentrations, but increasing concentrations of nitrate and nitrite were correlated with an increase in the ratio of N2O to total N gases. The results of Palmer et al. (2012) are especially surprising because typically the interior of a sorted/non-sorted circles would not be considered an environment favouring denitrification activity. However, others have found exceptionally high carbon (Wilson and Humphreys, 2010) fluxes from these environments and N cycling (Kaiser et al., 2005). Wilson and Humphreys (2010) suggested that this increased activity arose due to the increased dissolved organic C and warmer soil temperatures found in the interior of circles. This increased activity, coupled with the observation that low pH and low electron donor availability favour increased ratios of N2O to total N gases when nitrate is not limiting (Schalk-Otte et al., 2000; Simsek and Cooper, 2002; van den Heuvel et al., 2010; Palmer et al., 2012) may explain the surprising results of Palmer et al. (2012).

Studies from within peatlands and fens at lower latitudes may provide insight into possible patterns of N2 emissions at higher latitudes. Gaseous N exchange rates quantified by the gas-flow helium incubation method in an undrained monolith fen in northern Poland that was characterized by hollows and tussocks, found the net N2 production in hollows (2.53 mg N m-2 h-1) was significantly higher than in tussocks (1.04 mg N m-2 h-1) (Roodroock et al., 2010). Following amendment by NO3-, at a rate similar to atmospheric NO3 deposition, hollows showed a drastic shift to net production of N2O, but a non-significant increase in N2 production. In tussocks only a minor increase of N2 and N2O production was observed after NO3+ addition. If similar processes occur in arctic landscapes, higher N emissions as N2 may be expected in lower lying topography with limited NO3 availability. Wray and Bayley (2007) took measurements of direct N2-flux from intact cores in gas-tight N-free chambers from a Canadian boreal peatland. N2 fluxes ranged from 2.14 to 4.19 mg N m-2 h-1 in marshes and 6.19–6.81 mg N m-2 h-1 in fens. Annual estimation of N gas fluxes showed that fluxes of N2 and N2O were not significantly different among months. However, N2O was a very small fraction of the denitrification product and other studies in both wetland and forest environments have found relatively small amounts of N2O vs. N2 flux.
(Delaune et al., 1998; Ruckaef et al., 2004; Kitzler et al., 2006). Due to a lack of data on N2 flux within arctic landscapes, we cannot draw any strong conclusions regarding the influence of topography on N2 emissions. Therefore, future studies aimed at capturing gaseous N input and output in terrestrial arctic environments need to consider measurement of N2 flux.

Relatively few studies provide a rigorous assessment of the microbial community coupled with rigorous measurements of N2O and N2 production rates. However, advances in molecular techniques also provide a means to better understand these flux processes by combining analysis of microbial ecology and quantification of N2O:N2 production and the partitioning of different microbial sources of N2O (Butterbach-Bahl et al., 2013). There are a number of genes that play a key role in the nitrification and denitrification processes. The amoA gene encodes the active site of ammonia monoxygenase, an enzyme unique to nitrifying bacteria and archaea. Oxidation of ammonia to nitrite is the first and rate-limiting step of nitrification (Banerjee and Siciliano, 2012a) and therefore, the role of both bacterial amoA and crenarchaeal amoA have been examined in several arctic studies (Ma et al., 2007; Siciliano et al., 2009; Lamb et al., 2011; Banerjee and Siciliano, 2012a). Several genes encode for the oxidoreductases involved in denitrification, such as encoding for 3-aminonitrous oxide reductases (nirK and nirS (encoding for copper and cytochrome cd1-containing nitrite reductases respectively), norBC (encoding for NO reductases) and nosZ (encoding for N2O reductases) (Zumft, 1997; Palmer et al., 2012). These genes are commonly used as structural markers for the analysis of nitrate reducer and denitrifier communities (Palmer et al., 2012) and have also been examined in several arctic studies (Walker et al., 2008; Siciliano et al., 2009; Lamb et al., 2011; Banerjee and Siciliano, 2012b; Palmer et al., 2012). Through comparison of amoA and nosZ prevalence and activity, the importance of nitrifiers in N2O emissions from arctic soils under field conditions has been identified and linked to the competition for nitrate between fungi and denitrifiers (Ma et al., 2007, 2008; Siciliano et al., 2009). Higher copy number of norG has been observed in cytoplasmated than uncytoplasmated peat soils (Palmer et al., 2012). In addition, the nirS:nirK−1 copy number ratios differ between these soils, suggesting that different N2O emissions patterns across cytoplasmated and uncytoplasmated soils are associated with different denitrifier communities (Palmer et al., 2012). As more sophisticated molecular techniques continue to be developed, the use of functional genes in examining N cycling will undoubtedly provide essential information in identifying key factors driving the various N transformations.

7.1. Vegetation and N2O flux in arctic ecosystems

Since the distribution of plants in arctic ecosystems is strongly related to topographical gradients (Chapin et al., 1991; Walker, 2000) the role that plants play in altering N flux cannot be ignored. The direct role that vegetation plays in altering N2O emissions and the mechanisms by which plants can alter N2O emissions in arctic ecosystems are still somewhat unclear (Stewart et al., 2012b). Some studies suggest N2O may be produced by nitrification in plants (Goshima et al., 1999; Smart and Bloom, 2001; Hakata et al., 2003). Smart and Bloom (2001) found N2O emitted in the transpiration stream from wheat leaves derived from direct N2O production by plant NO3 assimilation and not from N2O produced by microorganisms on root surfaces. N2O emissions via evapotranspiration can occur when N2O dissolved in soil water evaporates and/or is taken up from the soil by roots and then released to the atmosphere via transpiration (Mosier et al., 1990; Chang et al., 1998; Ruch and Renningen, 1998; Piblatie et al., 2005; Chapuis-Lardy et al., 2007). Plants leaves may directly absorb N2O from the atmosphere and even metabolize small portions of the N absorbed (Li et al., 2011; Stewart et al., 2012b) (Fig. 1: pathway h). Studies examining the direct impact of vegetation on N2O emissions are limited to agricultural crops and there is a knowledge gap concerning the influence of arctic vegetation on N2O and N2 emissions.

Indirectly, plants influence N2O emissions via belowground competition for mineral N. There are higher N2O emissions from vegetation-free tundra peat circles, likely due to a lack of competition for mineral N belowground (Repo et al., 2009). Competition between roots and denitrifiers, especially when nitrate levels are low could result in lower rates of denitrification. Alternatively, bacteria isolated from root surfaces are known to release nitric oxide when metabolizing nitrate and the presence of live roots stimulates denitrification (Klemedtsson et al., 1999), Roobroeck et al. (2010) found tussocks acted as a source of N2O, while barren hollows with lower root density acted as N2O sinks. Similarly, Stewart et al. (2012b) found moss-dominated communities acted as N2O sinks while willow communities, which would have higher root densities, acted as sources. This suggests that evapotranspiration is a key mechanism by which plants contribute to N2O flux because the willow can access groundwater whereas moss cannot. The stimulation of denitrification in the rooting zone is often attributed both to root respiration that decreases oxygen contents and to the exudation of easily metabolized organic compounds by the roots, which in turn may be used as an energy source by denitrifying bacteria. It may be that on exposed beach ridges or other barren high topographical positions, lower belowground biomass could influence lower N emissions via a soil-plant-atmosphere pathway. However, findings are often contradictory suggesting that roots may decrease, as well as stimulate denitrification (Smith and Tiedje, 1979; Klemedtsson et al., 1999) (Fig. 1: pathway i). The variability of N2O and N2 fluxes measured at the soil-atmosphere interface may be better explained with more understanding of plant–microbe interactions in the rhizosphere (Butterbach-Bahl et al., 2013).

Several studies suggest that zones of production and consumption change throughout the soil profile (Kellman and Kavanagh, 2008; Jørgensen et al., 2011; Brummell et al., 2012). Nitrous oxide production, consumption and transport can vary markedly with depth of only a few centimetres (Ball et al., 1997). Jørgensen et al. (2011) found N2O sinks were largest in the top soil and rhizosphere through which N2O produced in deeper soil layers must pass (Fig. 1: pathway g). The depth of N2O production within the soil profile can influence the net positive or negative flux measured at the soil surface (e.g., Clough et al., 1999; Verchot et al., 1999; Brye et al., 2001; Elmi et al., 2003; Müller et al., 2004) because N2O is not conserved as it moves through the soil profile, and can be readily consumed by denitrifying bacteria. Light may also influence N2O flux through resource competition between vegetation and soil microbes in response to light-driven changes in O2 availability (Jørgensen et al., 2012; Stewart et al., 2012b). Stewart et al. (2012b) observed individual plant communities in an arctic ecosystem that shifted between N2O sinks and sources depending on light conditions. In addition to light-driven belowground processes, aboveground internal N2O production in plants may play an important role. Not only has light-dependent plant internal N2O production been hypothesized to occur within the aboveground biomass of some higher plants (Yu and Chen, 2009), but stomatal activity that is influenced by light may control N2O release processes (Li et al., 2011). The different relationships between environmental factors and N2O flux under light and dark conditions observed in some studies suggest complex interactions between plant communities and abiotic factors controlling N2O flux (Li et al., 2011; Stewart et al., 2012b).
Plant-mediated N₂O flux appears to play an important role in net N emissions in arctic ecosystems. Therefore, not only are changes in soil moisture and temperature likely to be key factors driving future N₂O emissions in the arctic, but enhanced shrub growth associated with climate warming trends in the Arctic (Goetz et al., 2005; Sturm et al., 2001; Tape et al., 2006, 2012) may also impact future plant-mediated N₂O emissions. There is a need for studies that not only improve our understanding of N₂O flux across the soil profile, but also studies that provide insight into plant-mediated N₂O emissions across topographical gradients.

8. Key questions for future research

- Rates of biological nitrogen fixation are available from several arctic studies, however, further quantification of total N input via both biological nitrogen fixation and atmogenic deposition in arctic landscapes is needed.
- The link between fixed N from cyanobacterial associations and soil fertility is unclear. While these associations fix substantial amounts of N in arctic ecosystems, it is not yet known how much of this fixed N influences the underlying soil profile and subsequently acts as a source of plant community N.
- The role of N₂-fixing associations in vegetation community changes that are being driven by climate change needs to be examined. For example, the significance of N₂ fixation by Alnus spp. in the shrub proliferation in the North Slope of Alaska is poorly understood.
- Competition between N₂-fixing organisms and arctic plants for limited N, P and micronutrients influences both N₂-fixation rates by N₂ fixers, as well as N availability for vascular plants. Further investigations are required to confirm the occurrence and consequences associated with these competitive interactions.
- Although, mineralization and immobilization of N is relatively insensitive to changes in temperature in the typical temperature range of an arctic soil. Nitrogen mobilization-immobilization in arctic soils may respond to climate driven perturbations and should be examined.
- There is a need to determine ecosystem-scale linkages between the prevalence of N₂ fixation and denitrification, as topographic controls on these processes are similar. The role of topographical gradients of N inputs and losses needs to be considered in the determination of N-mass balance calculations in arctic landscapes.
- The impact of thawing permafrost on gaseous N exchange requires attention. Alteration of surface moisture conditions, especially in low topographic areas, due to melting permafrost may have an important influence on N₂ fixation. In addition, changes in active layer depth and moisture conditions across the soil profile may strongly affect N₂O and N₂ flux in the arctic.
- The regulation and composition of soil nitrifier and denitrifier communities in the arctic will likely be different in these low N content soils compared to the heavily N impacted soils at lower latitudes. More work is needed to understand the composition and regulation of microbial communities that oxidize ammonia and reduce nitrate in these cold, low N environments.
- Little to nothing is known about heterotrophic nitrification or fungal denitrification processes occurring in arctic soils. More work is needed to link the denitrification and nitrification pathways in arctic environments and provide insight into the role of heterotrophic nitrifiers and fungal denitrifiers.
- The short term influence of plant metabolism on gaseous N movement needs to be better understood. The influence of belowground rooting systems of some arctic plants likely influences N₂O flux through competition for mineral N. N movement and metabolism within the aboveground portion of plants has a small, but significant effect on N₂O flux. More work is needed to understand the influence of belowground plant biomass and plant physiology that is giving rise to this phenomenon.
- Determining N-mass balance in arctic ecosystems is needed, especially within context of determining the influence of climate change on driving arctic ecosystems to act as net sources or sinks of reactive nitrogen.

9. Conclusions

The presence and importance of each of the N pathways discussed here is highly dependent on the environmental and edaphic conditions at and within a given site. However, there are a number of drivers, including precipitation, soil moisture, temperature, light, SOM and N and C substrate availability that play a key role in determining N input, cycling and output across the Arctic. Topography is an overriding control on many of these factors through establishing elevation gradients that result in spatial variation in resource availability and in turn influence the presence and rates of N transformation processes. While incorporation of environmental conditions into global change models, including moisture, temperature and light, are likely key for wider-scale modelling, inclusion of topographic variables may substantially increase landscape and regional scale model accuracy and may be more appropriate for the current spatial scale resolution of global models. In our review of gaseous N exchange in arctic ecosystems it is clear that factors driving variation in N₂-fixation rates in arctic landscapes are conceptually well understood, however, they are often poorly quantified. Gaseous N emissions across the landscape and between different vegetation communities require further investigation, not only due to a lack of quantification but also due to a poor understanding of the complex underlying mechanisms driving variation. In summary, there are several critical unknowns regarding N input, cycling and output within arctic ecosystems. The following techniques, tools and research strategies provide a means to address key knowledge gaps: i) employment of molecular techniques for further characterization of functional gene expression involved in N₂-fixation, nitrification and denitrification and insight into key factors driving N transformations, ii) determination of the importance of biologically fixed N as a source of N for arctic plants, iii) better characterization of vertical (soil profile) and horizontal spatial patterns of N₂O flux and the mechanisms associated with these emissions, especially for N₂O sinks, iv) determination of the relative importance of nitrifier denitrification and denitrification and identification of the key driving factors for these two pathways and v) examination of the direct role that vegetation plays in altering N₂O flux and the mechanisms by which arctic plants can alter N₂O flux.

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