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Review paper

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

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ABSTRACT

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 N_2-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. N_2-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. N_2-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 nitrification and immobilization tend to be inhibited in these locations. This higher mineralization is linked to relatively high N_2O emissions in lower lying areas in arctic landscapes since moisture and NH_4 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 N_2O 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.

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, NH_4^+, NO_3^- and NO_2^- and PO_4^{3-} (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 N_2O) through their influence on soil microbial processes (Stewart et al., 2012a; Brummell et al., 2012). Arctic ecosystems appear to be more

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responsive to additions of N and P than to changes in temperature, light or carbon dioxide (CO_2) (Henry et al., 1986; Chapin et al., 1995; Hobbie and Chapin, 1998; Shaver et al., 1998; van Wijk et al., 2003; Hill and Henry, 2011). 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 N_2 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 50–80% 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} yr^{-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} yr^{-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} (NADP, 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, photoheterotrophic 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

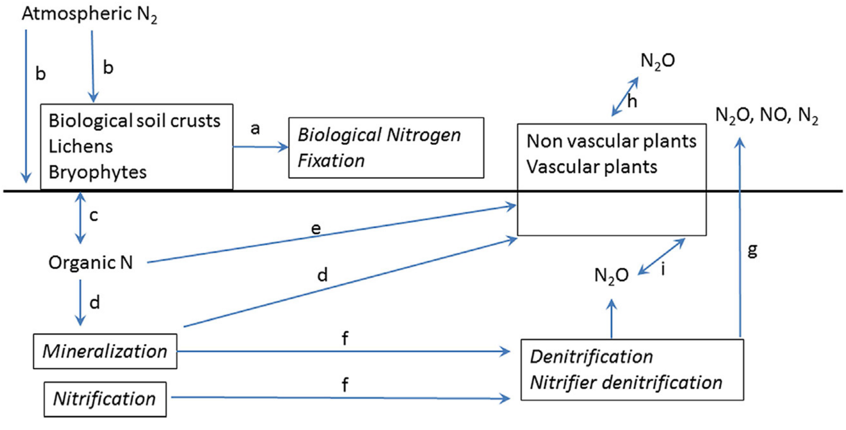

Fig. 1. N input, cycling and output pathways influencing gaseous N exchange in arctic ecosystems including surface biological N_2-fixation (a), atmospheric deposition (b), release and uptake of organic N from N_2-fixers (c), vascular plant uptake of inorganic N (d), vascular plant uptake of organic N (e), Inorganic N as a source of substrate for denitrification and nitrifier denitrification (f), Gaseous N emissions from the soil (g), N_2O flux from plants via evapotranspiration and passive pathways (h), and N_2O flux in the rhizosphere (i).

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 cyanobacteria 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 N_2-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 N_2-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 Vitousek, 1999). *Stereocaulon* spp., *Peltigera* spp. and *Nephroma arcticum* are common cyanolichens in arctic ecosystems and have N_2-fixation rates often exceeding that of other cyanobacterial symbioses (Alexander and Schell, 1973; Hobara et al., 2006). For example, *Stereocaulon paschale* had rates of N_2-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 N_2-fixation (Fig. 2).

Bryophytes influence N_2-fixation in many ecosystems by forming facultative associations with cyanobionts (DeLuca et al., 2002; Turetsky, 2003). *Pleurozium schreberi*, *Hylocomium splendens*, *Bryum* spp., *Sphagnum* spp., *Racomitrium lanuginsoum*, *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. *Oxytropis* spp. and *Astragalus* spp.) and *Rhizobium*-type bacterial root nodules, and between *Dryas* spp. and *Frankia*-type bacterial root nodules, as well as between bacterial N_2-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, N_2-fixation by *Oxytropsis* spp. and *Dryas octopetala* can be high on a plant dry weight basis ($\sim$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

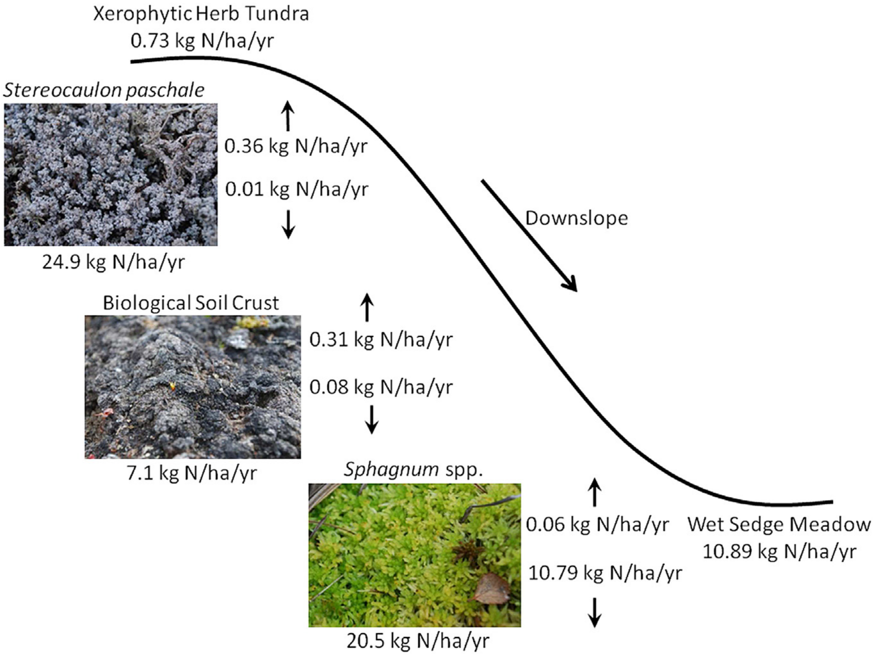

Fig. 2. Nitrogen fixation in an arctic tundra landscape at Daring Lake, NWT. The three main nitrogen fixing associations (*Stereocaulon paschale*, Biological Soil Crusts and *Sphagnum* spp.) are given with their mean growing season N_2-fixation rate under field conditions (below photograph). Arrows indicate the relative contribution of each nitrogen fixing associations based on the mean N_2-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.

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 N_2-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 N_2-fixation and is encoded by *nif*D, *nif*K and *nif*H 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 *nif*HDK operon is a good marker for N_2-fixing conditions (Zehr et al., 2003). All N_2-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 O_2 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-Karlsson et al., 2003; Weiss et al., 2005; DeLuca et al., 2008; Zackrisson et al., 2009; DeLuca et al., 2008).

Very few studies have investigated *nif*H gene distribution or activity in terrestrial arctic environments. Deslippe and Egger (2006) provided the first examination of *nif*H 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 *nif*H sequences indicated that *nif*H gene diversity in polar plant communities is largely unknown. Site factors including plant community composition, soil characteristics, moisture and temperature are the main determinant of *nif*H community structure (Walker et al., 2008). The response of the *nif*H 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 *nif*H prevalence in relation to rates of N_2-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 *nif*H abundance was related to microtopographical gradients. Hollow BSCs had higher growing season N_2-fixation rates, higher growing season *nif*H abundance, higher total % N and $\delta^{15}N$ values closer to that of atmospheric N_2, all of which suggest that N_2-fixation inputs are larger in the hollows of hummock-hollow ecosystems.

4. Environmental controls on N_2-fixation

N_2-fixation rates at any location depend on the distribution of N_2-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 N_2-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 N_2-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.

Ecosystem type	Location	Study	Precipitation (%)	Temperature (%)	Light (%)	N_2-fixation downslope (%)	Higher N, C, pH (%)
Boreal-arctic forest, Tundra	69°45′N, 27°01′E 71°20′N 156°38′W	Alexander and Schell, 1973; Schell and Alexander, 1973; Alexander et al., 1978	+	+	+23	+T 17, +MT ~ 50–75	
Tundra mire	68°21′N 19°05′E	Granhall and Selander, 1973; Basilier and Granhall, 1978		+OT 16–20	+		+pH
Boreal-arctic forest	60°21′N 106°54′W	Crittenden and Kershaw, 1978	+		+		
Coastal tundra	71°17′N 156°45′W	Gersper et al., 1980	+			+T 96	
High arctic lowland	78°53′N 75°55′W	Henry and Svoboda, 1986				+MT 75	
High arctic lowland	75°33′N 84°40′W	Chapin et al., 1991	+	+OT ~20	+	+T ~84–89	
High arctic lowland, Tundra mire, Alpine heath	78°53′N 75°55′W 69°45′N, 27°01′E etc.	Chapin and Bledsoe, 1992	+20	+OT 15–25	+5	+T ~80–90	
High arctic lowland	75°33′N 84°40′W	Lennihan et al., 1994		+OT 15–19			
Low arctic alpine	68°08′N 151°45′W	Nash and Olafsen, 1995	+	+OT ~ 20			
Polar desert	78°5′N 11°6′E	Liengen and Olsen, 1997a; Liengen, 1999a	+	+OT 19–24			+pH
Polar desert	75°33′N 84°24′W	Dickson, 2000	+	+OT 24			
Boreal-arctic forest	68°35′N 18°82′E	Solheim et al., 2002	+83				
High arctic lowland	78°47′N 16°19′E	Zielke et al., 2002, 2005	+	+OT 25–32	+		
Tussock tundra	68°37′N 149°18′W	Hobara et al., 2006		+OT 30+	+ ~45	−T ~ 25	
Low arctic alpine	61°10′N 138°26′W	Marsh et al., 2006	+	+OT 25°			+MN 82, +TN 53, +TC 67
Tundra	68°19′N 18°51′E	Sorensen et al., 2006		+OT 20–32	+		
Polar desert	79°10′N 79°45′W	Breen and Levesque, 2008					+OC 96, +N, +pH
Low arctic tundra	64°50′N 111°38′W	Stewart et al., 2011b				+MT 35	+TN, +NH_4, +NO_3

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 N_2-fixation compared with other temperatures (°C). MN = Mineralizable Nitrogen, TN = Total Nitrogen, TC = Total Carbon, OC = Organic Carbon.

1997a; Zielke 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 N_2-fixation and N biogeochemical cycling in northern landscapes (Table 1; Fig. 3).

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 N_2-fixation across various arctic ecosystems (Alexander, 1974; Alexander et al., 1978; Davey, 1983; Chapin and Bledsoe, 1992; Line, 1992; Zielke 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 N_2-fixation rates in arctic environments (Chapin and Bledsoe, 1992; Table 1). Seasonally, overall N_2-fixation rates are lower during summers with low rainfall (Gersper et al., 1980). Correlation of N_2-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 N_2-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 N_2-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 N_2-fixation under these drier conditions (Hobara et al., 2006; Table 1). However under moist conditions, higher rates of N_2-fixation are generally associated with lower positions within arctic landscapes with an increase in N_2-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 N_2-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 N_2-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 N_2-fixation in the Arctic vary from 15 to 30 °C (Alexander, 1974; Kallio and Kallio,

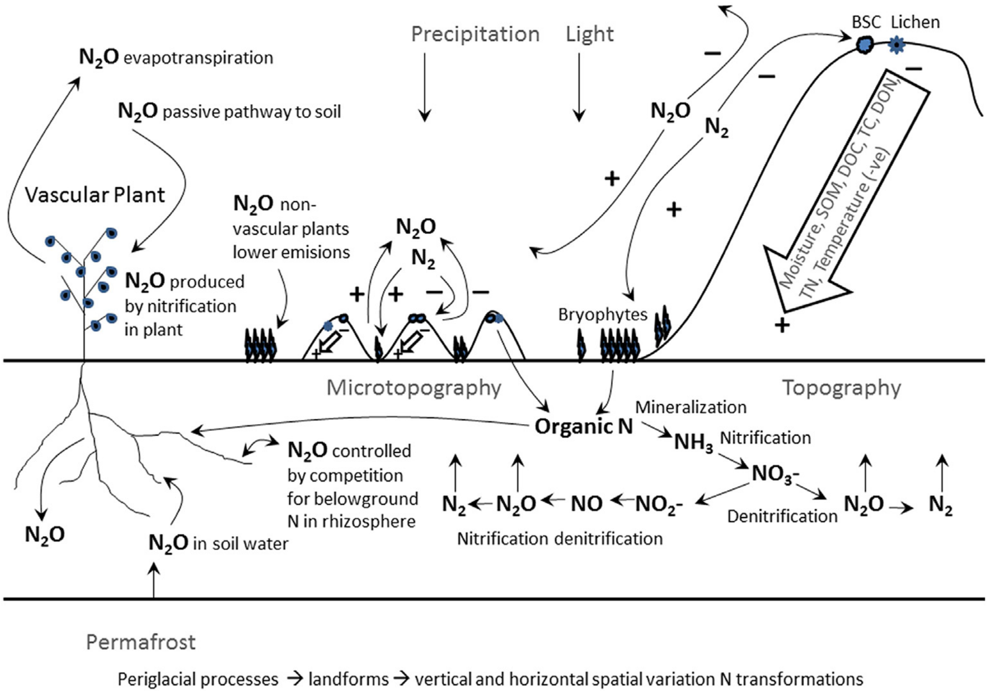

Fig. 3. Key factors controlling gaseous N input and output pathways in arctic ecosystems. Topography and microtopography are associated with abiotic gradients of higher soil moisture, soil organic matter (SOM), dissolved organic carbon (DOC), total carbon (TC), dissolved organic nitrogen (DON) and total nitrogen (TN) and lower soil temperature downslope. These gradients drive higher N_2-fixation rates (N_2) and N_2O emissions (N_2O) in lower-lying areas. The influence of non-vascular plants and the above and belowground systems of vascular plants on N_2O exchange are noted.

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.

Ecosystem type	Location	Study	Lower topographic or microtopographical position						
			Soil moisture (%)	Soil temperature (%)	Soil organic matter (%)	C, N, C:N (%)	Mineralization/ Immobilization (%)	Nitrification (%)	N_2O flux (%)
Coastal tundra	71°17′N 156°45′W	Gersper et al., 1980	+40–43	+5–19				−NN 37 *-SM*	+*C*
Tussock tundra	68°46′N 148°51′W	Giblin et al., 1991	+15–67		+HD 63–91	+N 49–88, +C 6–8), −C:N 22–45	+NM 0–80	+NN 20–79	
Tussock tundra	68°45′N 148°51′W	Nadelhoffer et al., 1991	+47–73		+HD 47–73	+N 76–91	+NM 73–92 +***T ~50–60***	+NP 83–94	
Willow-herb hummock and wet sedge tundra	75°33′N 84°40′W	Chapin, 1996	+52					−NN 84 −***pH,*** −***SM***	−76 +***NO_3***
Low shrub-moss-lichen tundra	66°23′N 65°28′W	Mueller et al., 1999	+~45	−47	+HD ~70	+C ~30, +N ~30			
Tussock tundra	68°38′N 149o38′W	Weintraub and Schimel, 2003				+N 30–71, +C 9	+ NM 46–99		
Tussock tundra	68°38′N 149°38′W	Schimel et al., 2004					+ NM 37, −I		
Tundra	72°42′N, 88°26′E 70°17′N 88°31′E	Biasi et al., 2005	+26–78	−18–53		+N 15–57, +C 14–60, +C:N 6–18, +NH_4 33–75, +NO_3 17–38, +MBN 58–60	+ GM 50–75, −GI 10–31		
Frost-boil tundra	69°43′N 74°39′E	Kaiser et al., 2005	+~65	−~20	+HD ~ 93	+C 85, +MBN ~ 75, +DON 45, +NH_4 58, +N 55–85, +C:N	+ NM 35, - GI 88		
Tussock tundra	68°37′N 149°18′W	Hobara et al., 2006	+~40–75						
High arctic lowland	75°40′N 84°35′W	Ma et al., 2007	+90–97			+NH_4 80–96, +NO_3 80–82			+64–87 +***NH_4,*** +***SM***
Tundra to polar desert	69°13′N, 148°84′W 78°79′N, 103°55′W	Michaelson et al., 2008	+5%			+C 80, +N 36, +C:N 20			
Low arctic tundra	64°50′N 111°38′W	Buckeridge et al., 2010b; Buckeridge et al., 2010a					***GM*** +***DOC,*** +***DON,*** −***litter C:N,*** −***SM,*** −***C***		+***N***
Low arctic tundra	64°50′N 111°38′W	Chu and Grogan, 2010	+52			−C:N ~40, +DON 43–67	+MP 97–99 +***TN,*** +***DOC,*** +***DON,*** +***NH_4,*** −***C:N***	+NP	
Low arctic tundra	64°50′N 111°38′W	Stewart et al., 2011b			+				
Boreal-arctic forest, Lichen-bryophyte-gramminoid tundra	58°45′N 93°51′W 75°33′N 84°40′W	Paré, 2011; Paré and Bedard-Haughn, 2012	+16–90	−13–63	+	+C 41–73, +DON 60–72, + NH_4 28, +NO_3 7, +N 18–68, +C:N 22	+ GM 51–79 +***C,*** +***N,*** +***NH_4,*** +***NO_3,*** +***GM,*** +***T***		
High arctic lowland	68°31′N 111°10′W 75°40′N 84°35′W	Banerjee and Siciliano, 2012a							+***N***

HD = Horizon Depth, only O and/or A depths considered, MBN = Microbial Biomass N, DON = Dissolved Organic Nitrogen, NM = Net Mineralization, MP = Mineralization Potentials, GM = Gross Mineralization, GI = Gross Immobilization, NN = Net Nitrification, NP = Nitrification Potential, DOC = Dissolved Organic Carbon, SM = Soil Moisture, TN = Total Nitrogen, T = Temperature, AOP = Ammonia Oxidation Potential, TOC = Total organic carbon.

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 C_2H_4:N_2 conversion ratio) (Davey and Marchant, 1983; Chapin et al., 1991; Chapin and Bledsoe, 1992; Lennihan et al., 1994; Zielke 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 little 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; Zielke 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 (Zielke 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 N_2 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 N_2-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 N_2-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 N_2-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 N_2-fixing organisms but also heterotrophs which, when N is scarce, will compete with vascular plants for this N (Fig. 1: pathway c). Thus, the relative abundance of microbes that can and cannot fix N_2 (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 NH_4^+ and NO_3^- deposited in summer rainfall (Crittenden, 1983, 1998) 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 phase of wetting, when cell wall integrity has not yet 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 N_2-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. CO_2 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; Fahnestock 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 N_2O 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 N_2O and N_2 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 N_2O and N_2 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). N_2-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 N_2-fixation may also promote denitrification (Chapin, 1996; Sorensen et al., 2006). Spatial correlations between N_2-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 N_2O 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 N_2O emissions (Ma et al., 2007; Elberling et al., 2010; Banerjee and Siciliano, 2012b; Brummell 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 N_2O emissions. Paré and Bedard-Haughn (2012) did not find significant differences in N_2O 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 N_2O 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 N_2O emissions were measured in low-lying wet sedge meadows (Gersper et al., 1980). Currently, there are only a few arctic studies examining N_2O flux across topographical gradients, however, in our review the majority of studies found significantly higher N_2O 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 N_2O emissions in arctic ecosystems. Labile C can affect soil denitrification by providing an energy source for denitrifying soil microbes in the production of N_2O 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 N_2O emissions, particularly in areas with high soil moisture and SOM, low soil inorganic N in arctic soils appears to limit N_2O emissions. For example, chronic high level NH_4–NO_3 fertilization elevated early springtime net N_2O 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 were 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 N_2O emissions with higher soil NO_3, NH_4 or total N (Table 2). Higher inorganic N availability in soils in lower lying areas may partly account for the higher rates of N_2O emissions detected there.

Previous studies from across the Arctic show very low N_2O emissions from many 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 N_2O sinks (Buckeridge et al., 2010a Paré and Bedard-Haughn, 2012; Stewart et al., 2012b). However, relatively few studies report net negative N_2O flux, especially under dry conditions like those found in polar deserts (Donoso et al., 1993; Yamulki et al., 1995; Klemedtsson 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 N_2O sinks are poorly understood. Net negative N_2O flux is not only dependent on the potential for N_2O reduction to N_2, but factors such as the diffusivity of N_2O within the soil profile and the dissolution of N_2O into soil water (Ryden, 1981; Chapuis-Lardy et al., 2007). Water-dissolved N_2O can be transported with drainage to other locations and generate N_2O emissions elsewhere, confounding the relationship between controlling factors in the soil and surface N_2O 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 N_2O emissions (Repo et al., 2009; Brummell et al., 2012).

6.1. *Denitrification and nitrifier denitrification in soils*

Most studies clearly indicate that higher N_2O emissions are detected in low-lying areas and this is often attributed to higher rates of denitrificaiton. Production of N_2O in soils can arise from different assimilative or dissimilative pathways (Stein, 2011). There are two main pathways by which N_2O and $N_2$are formed in arctic ecosystems: denitrification and nitrifier denitrification (Fig. 1: pathway g). Denitrification is the respiratory reduction of NO_3^- and NO_2^- to N_2O and N_2 (Tiedje, 1994). Net N_2O consumption during denitrification by denitrifying bacteria can occur, reducing N_2O to N_2 (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 N_2O to N_2 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 O_2 availability and N substrate availability are the main controlling factors. Nitrification is an aerobic process, however nitrifier denitrification occurs when O_2 availability is limited and nitrifiers use nitrite as an electron acceptor producing NO and N_2O (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 N_2O in temperate systems (Dalal and Allen, 2008), recent studies suggest that N_2O 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 N_2O from these processes would be less than that from denitrification under ideal conditions in which denitrifiers did not compete for NO_3^- but under typical soil conditions, competition for NO_3^- severely limits denitrification compared to nitrification activity (Siciliano et al., 2009). Higher rates of N_2O emissions generally occur at lower topographical or microtopographical positions and these emissions may be driven by the nitrifier denitrification pathways. Saturated soil conditions typical of low-lying areas may allow for nitrous oxide reductase to always be fully active, and therefore denitrifiers likely contribute little to N_2O flux. In contrast, under the moisture-limited conditions that occur in higher topographical positions, N_2O reductase is not fully induced and therefore denitrifier activity is likely the main determinant of N_2O flux (Stewart et al., 2012a).

The influence of hydrological gradients associated with topography on N_2O 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 N_2O 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 N_2O emissions in a high arctic wet sedge meadow decreased with decreasing soil NH_4, and that NH_4 rather than NO_3 correlated with cumulative N_2O flux. Our review indicates that N mineralization and N_2O fluxes tend to be largest in relatively low-lying areas in arctic landscapes.

While mineralization rates and NH_4 availability likely play an important role in N_2O flux via the nitrifier denitrification pathway, there is also evidence that NO_3 and nitrification contribute to N_2O emissions (Table 2). For example, the soil N cycle was closely linked to N_2O emissions via nitrification in a high arctic wet sedge meadow but via NO_3–N in a high arctic *Dryas* spp. dominated heath ecosystem (Stewart et al., 2012a). The direct influence of inorganic N and in particular NO_3–N on N_2O emissions likely indicates a nitrification-coupled denitrification pathway (i.e. N_2O produced from denitrifiers by reduction of NO_3-produced from nitrification) as the primary source of N_2O emissions (Ma et al., 2008; Kool et al., 2011; Stewart et al., 2012a). Increased N cycling rates promote nitrification, which either directly releases N_2O (Ma et al., 2007, 2008) or in turn stimulates denitrification which also releases N_2O (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; Banerjee and Siciliano, 2012a) while others reported low or negligible nitrification rates (Rosswall and Granhall, 1980; Chu and Grogan, 2010). Low pH (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;

Chu and Grogan, 2010). 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, O_2 availability and N substrate are key factors influencing overall N_2O 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). N_2O 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 N_2O whereas increasingly anaerobic conditions increase denitrification activity which releases N_2O. 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 (^{18}O, ^{15}N) may offer a means to examine the contribution of different microbial processes (Baggs, 2008). N_2O produced during nitrification is more depleted in ^{15}N and ^{18}O relative to N_2O produced during denitrification, however isotopic techniques have not yet been applied to distinguish between all known microbial sources of N_2O 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 N_2O production by oceanic ammonia-oxidizing archea (AOA) (Santoro et al., 2011) indicate that while AOA can contribute to N_2O 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 N_2O 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 N_2O 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 N_2O production in AOBs are the same as those leading to N_2O production in AOAs.

7. N_2 emissions

There are relatively few studies that provide measurement of N_2 emissions and to our knowledge only one study that specifically addresses N_2 emissions within an arctic terrestrial environment (Palmer et al., 2012). In general, this scarcity is primarily due to the methodological problems of measuring N_2 production via denitirification and disentangling N_2O production processes at a field scale (Groffman et al., 2006; Butterbach-Bahl et al., 2013). Acetylene inhibition methods have been used to quantify $N_2O + N_2$ production by inhibiting N_2O reduction to N_2 via denitrification (Klemedtsson et al., 1988; Kitzler et al., 2006). However, under aerobic conditions the acetylene inhibition method is known to produce underestimation of N_2 production by denitrification and $N_2O{:}(N_2O + N_2)$ 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 N_2 following the application of ^{15}N-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 PO_2 when removing N_2, and a fertilization effect respectively. Butterbach-Bahl et al., 2013 summarized all available datasets where N_2 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 N_2O from nitrification versus denitrification rather than as a means to effectively quantify N_2 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 denitrifiers and N_2O as the main end product of denitrification. However, in cryoturbed peat soils, N_2O that was initially produced from internal-N sources was consumed, indicating the capability of peat soil denitrifiers for complete denitrification to N_2 under acidic conditions. Ratios of N_2O 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 N_2O 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 Humphrey (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 N_2O to total N gases when nitrate is not limiting (Schalk-Otte et al., 2000; Simek 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 N_2 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 N_2 production in hollows (2.53 mg N m^2 h) was significantly higher than in tussocks (1.04 mg N m^2 h) (Roobroeck et al., 2010). Following amendment by NO_3^-, at a rate similar to atmospheric NO_3^- deposition, hollows showed a drastic shift to net production of N_2O, but a non-significant increase in N_2 production. In tussocks only a minor increase of N_2 and N_2O production was observed after NO_3^- addition. If similar processes occur in arctic landscapes, higher N emissions as N_2 may be expected in lower lying topography with limited NO_3^- availability. Wray and Bayley (2007) took measurements of direct N_2-flux from intact cores in gas-tight N-free chambers from a Canadian boreal peatland. N_2 fluxes ranged from 2.14 to 4.19 mg N m^2 h in marshes and 6.19–6.81 mg N m^2 h in fens. Annual estimation of N gas fluxes showed that fluxes of N_2 and N_2O were not significantly different among months. However, N_2O was a very small fraction of the denitrification product and other studies in both wetland and forest environments have found relatively small amounts of N_2O vs. N_2 flux

(Delaune et al., 1998, Ruckauf et al., 2004; Kitzler et al., 2006). Due to a lack of data on N_2 flux within arctic landscapes, we cannot draw any strong conclusions regarding the influence of topography on N_2 emissions. Therefore, future studies aimed at capturing gaseous N input and output in terrestrial arctic environments need to consider measurement of N_2 flux.

Relatively few studies provide a rigorous assessment of the microbial community coupled with rigorous measurements of N_2O and N_2 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 N_2O:N_2 production and the partitioning of different microbial sources of N_2O (Butterbach-Bahl et al., 2013). There are a number of genes that play a key role in the nitrification and denitrification processes. The *amo*A gene encodes the active site of ammonia monooxygenase, an enzyme unique to nitrifying bacteria and archea. 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 *amo*A and crenarcheal *amo*A 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, including *nar*G or *nap*A (encoding for dissimilatory nitrate reductases), *nir*K and *nir*S (encoding for copper and cytochrome cd_1-containing nitrite reductases respectively), *nor*BC (encoding for NO reductases) and *nos*Z (encoding for N_2O 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 *amo*A and *nos*Z prevalence and activity, the importance of nitrifiers in N_2O 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 *nar*G has been observed in cryoturbated than unturbated peat soils (Palmer et al., 2012). In addition, the *nir*S:*nir*K^{-1} copy number ratios differ between these soils, suggesting that different N_2O emissions patterns across cryoturbated and unturbated soils are associated with different denitrifer 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 N_2O 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 N_2O emissions and the mechanisms by which plants can alter N_2O emissions in arctic ecosystems are still somewhat unclear (Stewart et al., 2012b). Some studies suggest N_2O may be produced by nitrification in plants (Goshima et al., 1999; Smart and Bloom, 2001; Hakata et al., 2003). Smart and Bloom (2001) found N_2O emitted in the transpiration stream from wheat leaves derived from direct N_2O production by plant NO_3 assimilation and not from N_2O produced by microorganisms on root surfaces. N_2O emissions via evapotranspiration can occur when N_2O 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; Rusch and Rennenberg, 1998; Pihlatie et al., 2005; Chapuis-Lardy et al., 2007). Plants leaves may directly absorb N_2O 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 N_2O emissions are limited to agricultural crops and there is a knowledge gap concerning the influence of arctic vegetation on N_2O and N_2 emissions.

Indirectly, plants influence N_2O emissions via belowground competition for mineral N. There are higher N_2O 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 N_2O, while barren hollows with lower root density acted as N_2O sinks. Similarly, Stewart et al. (2012b) found moss-dominated communities acted as N_2O 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 N_2O 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 N_2O and N_2 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 Kavanaugh, 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 N_2O sinks were largest in the top soil and rhizosphere through which N_2O produced in deeper soil layers must pass (Fig. 1: pathway g). The depth of N_2O 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 N_2O is not conserved as it moves through the soil profile, and can be readily consumed by denitrifying bacteria.

Light may also influence N_2O flux through resource competition between vegetation and soil microbes in response to light-driven changes in O_2 availability (Jørgensen et al., 2012; Stewart et al., 2012b). Stewart et al. (2012b) observed individual plant communities in an arctic ecosystem that shifted between N_2O sinks and sources depending on light conditions. In addition to light-driven belowground processes, aboveground internal N_2O production in plants may play an important role. Not only has light-dependent plant internal N_2O 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 N_2O release processes (Li et al., 2011). The different relationships between environmental factors and N_2O flux under light and dark conditions observed in some studies suggest complex interactions between plant communities and abiotic factors controlling N_2O flux (Li et al., 2011; Stewart et al., 2012b).

Plant-mediated N_2O 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 N_2O 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 N_2O emissions. There is a need for studies that not only improve our understanding of N_2O flux across the soil profile, but also studies that provide insight into plant-mediated N_2O 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 N_2-fixing associations in vegetation community changes that are being driven by climate change needs to be examined. For example, the significance of N_2 fixation by *Alnus* spp. in the shrub proliferation in the North Slope of Alaska is poorly understood.
- Competition between N_2-fixing organisms and arctic plants for limited N, P and micronutrients influences both N_2-fixation rates by N_2 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 N_2 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 N_2 fixation. In addition, changes in active layer depth and moisture conditions across the soil profile may strongly affect N_2O and N_2 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 denitification 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 denitifiers.
- 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 N_2O flux through competition for mineral N. N movement and metabolism within the aboveground portion of plants has a small, but significant effect on N_2O 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 N_2-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 N_2-fixation, nitrification and denitrification and insight into key factors driving N transformations, ii) determination of the importance of biologically fixed N_2 as a source of N for arctic plants, iii) better characterization of vertical (soil profile) and horizontal spatial patterns of N_2O flux and the mechanisms associated with these emissions, especially for N_2O 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 N_2O flux and the mechanisms by which arctic plants can alter N_2O flux.

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