Soil Biology & Biochemistry 70 (2014) 96–112

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Review paper

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

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ARTICLE INFO

Article history:
Received 26 April 2013
Received in revised form
4 December 2013
Accepted 6 December 2013
Available online 25 December 2013

Keywords:
Nitrogen
Nitrous oxide
Nitrogen fixation
Nitrogen cycling
Mineralization
Nitrification
Denitrification
Nitrifier denitrification
Arctic
Soil

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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http://dx.doi.org/10.1016/j.soilbio.2013.12.005

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

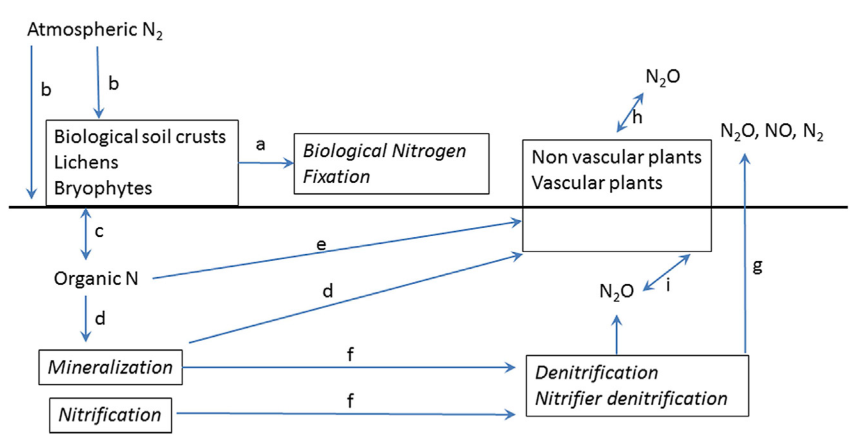

Fig. 1. N input, cycling and output pathways influencing gaseous N exchange in arctic ecosystems including surface biological N_2-fixation (a), atmospheric deposition (b), release and uptake of organic N from N_2-fixers (c), vascular plant uptake of inorganic N (d), vascular plant uptake of organic N (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).