Soil Biology & Biochemistry 43 (2011) 133–140

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

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

Small-scale spatial patterns in N_2-fixation and nutrient availability in an arctic hummock–hollow ecosystem

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ARTICLE INFO

Article history:
Received 18 May 2010
Received in revised form
13 August 2010
Accepted 17 September 2010
Available online 20 October 2010

Keywords:
Nitrogen fixation
Soil nitrogen
Phosphorus limitation
Nutrient availability
Low arctic
N_2-fixing cyanobacteria
Biological soil crusts

ABSTRACT

Atmospheric nitrogen that is fixed by associative cyanobacteria can be released into the surrounding soil environment providing a key source of N for arctic ecosystems. Yet, little is known about nitrogen fixation by Biological Soil Crusts (BSCs) within hummock-hollow complexes that are typical of many arctic environments. In this study, we examined spatial and temporal patterns in N_2-fixation, dinitrogenase reductase (*nif*H) gene abundance and release of N in a low arctic hummock-hollow ecosystem. The impacts of cyanobacteria on N status in soil were evaluated by assessing soil nitrogen in relation to the cyanobacterial associations found on Hummock and Hollow BSCs. In addition, potential P limitation of N_2-fixation by cyanobacteria was assessed for Hummock and Hollow BSCs. The tops of hummocks and the bottoms of hollows were areas of high N_2-fixation, whereas minimal N_2-fixation occurred on the sides of hummock–hollow complexes. Compared with Hummock BSCs, Hollow BSCs had a higher mean growing season N_2-fixation rate, a higher mean growing season *nif*H abundance, a higher mean total %N and $\delta^{15}N$ values closer to that of atmospheric N_2. Soil N status was linked to rates of N_2-fixation by BSCs indicating that these N_2-fixing associations act as important point sources of soil N in this low arctic ecosystem. Over the course of a growing season temporal variation in N_2-fixation and *nif*H abundance were weakly linked suggesting that N_2-fixation was carried out by complex communities of diazotrophic microorganisms and that factors such as nutrient availability may limit N_2-fixation to a greater extent than *nif*H abundance.

1. Introduction

Atmospheric N_2-fixation is a main source of N input in arctic ecosystems (Bazely and Jefferies, 1989; Chapin and Bledsoe, 1992; Hobara et al., 2006). Up to 70% of the N_2 fixed by associative cyanobacteria can be released into the surrounding soil environment providing a key source of N for soil ecosystems (Alexander and Schell, 1973; Harper and Belnap, 2001; Mayland and McIntosh, 1966; Stewart, 1967). In arctic environments N_2 fixed by cyanobacteria can provide readily available N (Alexander et al., 1978; Chapin and Bledsoe, 1992) but there is high spatial variability in N_2-fixation (Gold et al., 2001), often due to landscape topography (Biasi et al., 2005; Mueller et al., 1999; Walker et al., 2004). Hummock–hollow complexes are common features in tundra ecosystems and provide a model system for investigating the influence of microtopography on N_2-fixation and the subsequent distribution of soil nutrients. Well-developed Biological Soil Crusts (BSCs) on hummocks and in hollows are important point sources of nitrogen within the landscape (Stewart et al., unpublished data). However, the small-scale spatial patterns of nutrient availability associated with these point sources are not well understood.

*nif*H is the gene that encodes for the Fe protein subunit of nitrogenase, the enzyme responsible for nitrogen fixation (Deslippe et al., 2005). Since, *nif*H is highly conserved among all diazotrophic groups it is an ideal molecular marker for N_2-fixing organisms. Assessment of the *nif*H abundance associated with BSCs in hummock–hollow complexes can provide important insights into temporal and spatial variability in N_2-fixation and the subsequent patterns of nutrient availability.

Most soil nutrients do not have a consistent spatial distribution across the ecosystem and soil chemistry varies among plant types and between microsites (Biasi et al., 2005; Housman et al., 2007). The role that various N_2-fixing associations play in altering nutrient availability remains controversial (Belnap, 2001; Johnson et al., 2005; Knowles et al., 2006; Lagerstrom et al., 2007). A variety of factors can affect the concentration of available nitrogen in the soil,

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doi:10.1016/j.soilbio.2010.09.023

including uptake by plants, immobilisation by microbes, soil temperatures, microtopography and time of year (Biasi et al., 2005; Veluci et al., 2006). Furthermore, rainfall intensity alters the influence of BSCs on soil N concentrations. Higher intensity rainfall events (i.e. high volume of precipitation over short time) result in greater amounts of N or C being released because organisms are not able to reassimilate losses (Crittenden, 1983; Wilson and Coxson, 1999). In general the greatest release of leachates occurs upon initial rewetting after a prolonged period of desiccation. Thus, a comparison of N availability below BSCs in hummock–hollow complexes and the release of nutrients upon rewetting can be used as an indication of the importance of N_2-fixing association type, microtopography and N cycling processes that can influence the N status of soils.

Although N limitation is often cited as the main factor limiting ecosystem productivity, the fixation of N may in turn be limited by phosphorus availability (Cole and Heil, 1981; Crews, 1993; Eisele et al., 1989; Smith, 1992). Phosphate is a limiting factor for N_2-fixation by cyanobacteria in arctic habitats (Basilier and Granhall, 1978; Chapin et al., 1991; Liengen, 1999). Cole and Heil (1981) suggest that close linkages between P and N cycling processes are related because of the large energy requirements of N transformations. Low phosphorus availability may reduce rates of photosynthesis, which in turn may inhibit nitrogenase by reducing photosynthate supplies and in particular the supply of ATP (Crews, 1993; Hartley and Schlesinger, 2002; Layzell, 1990).

The objective of this study was to examine spatial and temporal patterns in N_2-fixation, *nif*H abundance and release of N in a hummock-hollow low arctic environment. We hypothesized that BSC N_2-fixation rates would be linked to soil N status and that the effect of BSC on soil fertility would differ between BSC type and location. Furthermore, we hypothesized that BSC N_2-fixation activity would be limited by P supply.

2. Methods

2.1. Study site and N_2-fixing associations

The study area was located in a low arctic tundra region at the Tundra Ecosystem Research Station, Daring Lake, Northwest Territories, Canada (64°52′N, 111°35′W). Elevation ranges from 414 to 470 m a.s.l. and landscape features include eskers, boulder fields, exposed bedrock, upland and lowland tundra, wetlands and various sizes of lakes, ponds and streams. Continuous permafrost is present at the site with a soil active layer ranging from 0.3 to 2 m (Obst, 2008).

Mean monthly air temperature in January is −30 °C and +13 °C in July (INAC, personal communication; Obst, 2008). Snow-melt usually starts after mid-May ending in early June, leaving some snow beds on slopes until late June or early July. The growing season usually occurs between the end of May or early June and ends after mid-August.

Located within the physiographic zone of the Bear-Slave Upland of the Canadian Shield, approximately 90 km northeast of the northern limit of continuous trees the Daring Lake study site is characterized as low arctic (Obst, 2008). Several ecosystem types including Xerophytic Herb Tundra, Heath-Lichen Tundra, Heath-Mat Tundra and Birch Hummock are present in the landscape and classification follows Obst 2008. The hummock–hollow complexes investigated were formed from cryoturbated mineral soil mounds approximately 30–50 cm in height and adjoining depressions of approximately the same depth. Complexes are often in groupings of several hummocks and hollows occupying an area of 1–5 m^2 occurring mainly within the Birch Hummock ecosystem type. Birch Hummock occurs in moderately to poorly-drained terrain on gentle lower esker slopes (Obst, 2008). Soils in the Birch Hummock ecosystem are classified as Orthic Dystic Turbic Cryosols, which consist of an organic layer above a silt-sand mineral layer (Buckeridge et al., 2009). Vegetation was characterized by scattered shrubs (0.2–0.5 m tall) of *B. glandulosa*, Cloudberry (*Rubus chamaemorus* L.), *Salix* spp., *Ledum decumbens* and tussock-forming Sheathed Cottongrass (*Eriophorum vaginatum* L.). Mosses (*Sphagnum* spp., *Ditrichum* sp., *Polytricum piliferum* Hedwig.), liverworts (*Anastrophyllum minutum* Schreb. and *Cephalloziella* spp.) and lichens (*S. paschale*, *Bryoria tenuis* (E. Dahl) Brodo & D. Hawksw., *Placynthiella uliginosa* Schrader. and *Cladonia* spp.) are also common.

Two major BSC communities were found in association with hummock–hollow microtopography. Hollow BSCs were found mainly in the depressions between hummocks and were composed of liverworts growing in dense mats generally underlain by varying depths of organic matter. The main components of Hollow BSCs were *Anastrophyllum minutum* Schreb. and *Cephalloziella* spp. including *C. rubella* (Nees) Warnst. and *C. hampeana* complex. Cyanobacteria were filamentous and heterocyst containing cyanobacterium *Stigonema cf. turfaceum* (Berk.) Cooke. However, on some samples filamentous and heterocyst *Tolypothrix* sp., and the filamentous, non-heterocystous *Schizothrix cf. cuspidata* W. et G.S. West., were found growing in between the leafy liverworts and on the *Stigonema* filaments. *Stigonema minutum* (C. Agardh) Hass. and *Calothrix* sp. were also found on Hollow BSC samples. Hummock BSCs were cohesive well-developed crusts (1–2 cm thick) found on cryoturbated mineral soil mounds. Small less well-developed patches of Hummock BSC also occurred in sandy well-drained areas on ridge tops. Hummock BSCs were complex communities made up of lichens, mosses and liverworts. Lichen species included *Placynthiella uliginosa* Schrader., *Bryocaulon divergens* Ach., *Bryoria tenuis* (E. Dahl) Brodo & D. Hawksw., *Cladonia* spp., *Japewia tornoensis* Nyl., *Ochrolechia frigida* Sw., and *Solorina crocea* L. Moss species (*Funaria* sp. *Pohlia* sp. *Ditrichum* sp. *and Polytricum piliferum* Hedwig.) and liverwort species (*Cephalozia* sp., *Cephaloziella* sp., *Anastrophyllum* sp., *Anthelia* sp., *Lophozia* sp. and *Lophozia incise* Schrad.) were also key components of these diverse communities. *Stigonema turfaceum*, *S. minutum* and *Stigonema hormoides* (Kutz.) Born. & Flah. were found on Hummock BSCs, however, *Gloeocapsa decorticans* (A. Braun) Ritcher., *Gloeocapsa novacekii* (Komárek & Anagnotid.), *S. cuspidata, Anabaena* sp. and *Chroococcidiopsis* sp. were also present.

2.2. N_2-fixation rates

Measurements of N_2-fixation were made using acetylene reduction assays (ARAs) (Stewart et al., 1967). Acetylene gas (C_2H_2) was generated on-site from CaC_2 and water, with incubations injected with 10% (v/v) acetylene. Ethylene concentrations were measured in the field with a portable gas chromatograph (SRI 8610A, Wennick Scientific Corporation, Ottawa, ON, Canada) fitted with a Porapak column (Alltech Canada, Guelph, ON, Canada) and a flame ionization detector. A stand-alone hydrogen generator (SRI H_2-50, Alltech Canada, Guelph, ON, Canada) provided hydrogen as the carrier gas, which was held at a constant pressure of 26 psi. Column temperature was held at 65 °C.

Cores (19 cm^2, 0.75 cm depth) of Hollow BSC ($n = 12$) and Hummock BSC ($n = 12$) were randomly selected at independent hummocks and hollows in the study site over the growing season (June 15th–16th, July 3rd–4th, August 7th–8th 2008). Samples were enclosed in 250 ml glass canning jars with rubber septa placed through a modified lid. For each set of incubations one sample for each N_2-fixing association was used as a control, which served as both a temperature control and a blank not injected with acetylene. Control samples did not show any natural evolution of ethylene.

Acetylene reduction assay (ARA) incubations were 6 h and occurred between 10:00–16:00 h. Photosynthetically active