Plant Soil (2011) 344:335–346
DOI 10.1007/s11104-011-0750-x

REGULAR ARTICLE

Bryophyte-cyanobacterial associations as a key factor in N_2-fixation across the Canadian Arctic

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Received: 17 October 2010 / Accepted: 15 February 2011 / Published online: 4 March 2011

Abstract Nitrogen inputs via biological N_2-fixation are important in arctic environments where N often limits plant productivity. An understanding of the direct and indirect theoretical causal relationships between key intercorrelated variables that drive the process of N_2-fixation is essential to understanding N input. An exploratory multi-group Structural Equation Modeling (SEM) approach was used to examine the direct and indirect effects of soil moisture, plant community functional composition, and bryophyte and lichen abundance on rates of nitrogen fixation at a low arctic ecosystem, two high arctic oases and a high arctic polar desert in the Canadian Arctic. Increasing soil moisture was strongly associated with an increasing presence of bryophytes and increasing bryophyte abundance was a major factor determining higher N_2-fixation rates at all sites. Shrubs had a negative effect on bryophyte abundance at all sites with the exception of the polar desert site at Alexandra Fjord highland. The importance of competition from vascular plants appears to be greater in more productive sites and may increase at lower latitudes. Moisture availability may have an indirect effect on ecosystem development by affecting N input into the system with bryophyte-cyanobacterial associations playing an important intermediary role in the process.

Keywords Arctic · Biological Soil Crust · Bryophyte · Climate change · Cyanobacteria · Lichen · Nitrogen fixation · Polar desert

Introduction

Nitrogen inputs via N_2-fixation are extremely important in arctic environments where N often limits plant productivity. The role of vegetation and environmental conditions in determining N_2-fixation rates for specific cyanobacterial species or N_2-fixing associations at a given site have been extensively studied (Schell and Alexander 1973; Crittenden and Kershaw 1978; Gunther 1989; Henry and Svoboda 1986; Chapin et al. 1991; Solheim et al. 1996; Dickson

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Responsible Editor: Euan K. James.

Electronic supplementary material The online version of this article (doi:10.1007/s11104-011-0750-x) contains supplementary material, which is available to authorized users.

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2000; Zielke et al. 2002, 2005; Hobara et al. 2006). Few studies, however, have simultaneously examined the relationships between environmental conditions, vascular plant communities, N_2-fixing associations and rates of N_2-fixation across several arctic sites varying widely in latitude and with diverse vegetation communities. In this study, approximately 400 samples with roughly 100 samples each taken from a high arctic upland polar oasis (Alexandra Fjord lowland), a high arctic polar desert (Alexandra Fjord highland), a high arctic wetland polar oasis (Truelove Lowlands) and a low arctic esker ecosystem (Daring Lake) were evaluated.

Cyanobacteria are ubiquitous in the Arctic where they are the primary source of newly fixed nitrogen (Alexander and Schell 1973; Alexander 1974; Granhall and Lid-Torsvik 1975; Henry and Svoboda 1986; Chapin et al. 1991; Chapin and Bledsoe 1992; Liengen 1999; Hobara et al. 2006; Solheim et al. 2006). Cyanobacteria form many associations with vegetation including epiphytic and endophytic facultative associations with bryophytes (Turetsky 2003) and the lichen symbioses and soil surface colonies that are components of Biological Soil Crusts (BSCs) (Belnap et al. 2001). Bryophyte-associated cyanobacteria are an important source of N within many terrestrial ecosystems. For example, a high abundance of feathermoss-cyanobacterial associations occur in northern boreal forests, where they contribute 1.5 to 2.0 kg N ha^{-1} yr^{-1} (DeLuca et al. 2002; Houle et al. 2006; Lagerström et al. 2007; Zackrisson et al. 2009). While variation is often high within and between bryophyte species, the highest rates of N_2-fixation in arctic landscapes are often associated with cyanobacteria bryophyte associations (Alexander and Schell 1973; Henry and Svoboda 1986; Solheim et al. 1996). Cyanobacterial symbioses with lichens are also a major source of fixed N as they often have N_2-fixation rates exceeding that of other cyanobacterial symbioses (Schell and Alexander 1973; Kallio and Kallio 1975; Crittenden and Kershaw 1978; Gunther 1989; Hobara et al. 2006). Finally, the prevalence of BSCs in many arctic ecosystems ensures that the cyanobacteria associated with those crusts are major contributors to arctic N inputs (Alexander and Schell 1973; Alexander et al. 1978).

The interactions between plant communities and environmental factors such as soil moisture can be important in determining both the establishment and survival of N_2-fixing associations and the rates at which they fix N_2. Soil moisture is not only important in structuring vegetation communities in the Arctic (Sohlberg and Bliss 1984; Oberbauer and Dawson 1992; Bliss et al. 1994; Gold and Bliss 1995a; Walker 2000), but is one of the most important environmental factors controlling N_2-fixation across many arctic environments (Alexander 1974; Alexander et al. 1978; Davey 1983; Chapin and Bledsoe 1992; Line 1992; Nash and Olafsen, 1995; Zielke et al. 2002, 2005; Convey and Smith 2006).

Vegetation functional types can play a major role in determining the moisture, light and temperature regimes under which N_2-fixing associations operate. Differences in the capacity of vegetation types to retain moisture and make it accessible to cyanobacteria have been correlated with rates of N_2-fixation (Zielke et al. 2002; 2005). Shading vegetation can reduce the light intensities available to an N_2-fixing association, and can limit the persistence of some lichens into later successional stages (Kershaw 1976; Foster 1985; Kurina and Vitousek 1999). Shading of N_2-fixing associations by shrubs may be particularly important given that remote sensing, repeat photography and experimental warming studies all suggest that current warming trends may be promoting shrub growth and expansion (Goetz et al. 2005; Sturm et al. 2001; Chapin et al. 1995; Walker et al. 2006). In addition, increased N availability and turnover under shrub canopies may act to down-regulate N_2-fixation (DeLuca and Zackrisson 2007).

An understanding of the contribution made by different N_2-fixing associations to N input across arctic environments is important. However, an understanding of the direct and indirect theoretical causal relationships between key intercorrelated variables that drive the process of N_2-fixation is essential to understanding current and future N input. In this study we used an exploratory multi-group Structural Equation Modeling (SEM) approach to examine the direct and indirect effects of soil moisture, plant community functional composition, and bryophyte and lichen abundance on rates of nitrogen fixation at four sites varying in latitude and vegetation type. The effects of these factors and the networks of interactions among them were compared across sites to determine the influence of different N_2-fixing associations on N_2-fixation and key interactions driving N_2-fixation across the Arctic.

Materials and methods

Site descriptions

The four study sites located across the Canadian Arctic ranged in latitude from 79°53′N to 64°52′N. Two high arctic sites were located ~5 km apart at Alexandra Fjord, Ellesmere Island, Nunavut Territory, one in a lowland polar oasis (78°53’N, 75°55’W) and the other in a highland polar desert (78°51’N, 76°06’W). A third high arctic site was located at Truelove Lowlands, Devon Island, Nunavut Territory (75°67’N, 84°58’W) and a low arctic site was located at Daring Lake, Northwest Territories (64°52’N, 111°35’W) (Fig. 1).

The Alexandra Fjord lowland site was in an 8 km^2 lowland oasis on the eastern side of central Ellesmere Island. The oasis is a deglaciated lowland delimited by a glacier to the south, cliffs and talus slopes (ca. 500 m) to the west and east and by the fjord waters to the north (Muc et al. 1989). Lowland soils are predominantly Regosolic Static Cryosols (Soil Classification Working Group 1998) that are generally coarse textured with variable concentrations of organic matter. Average air temperature is −15°C and mean monthly air temperature in July is 4.5°C (Labine 1994). Annual precipitation at Alexandra Fjord lowland is<60 mm with<10 mm falling during the growing season from mid-June to August (Muc et al. 1989). The lowland has an extensive vegetation cover dominated by deciduous dwarf shrubs, heaths, cushion plants and hydric sedges. Transects were placed over relatively flat terrain with the presence of some hummocky areas where Dwarf shrub-Cushion Plant communities were dominant (follows Muc et al. 1989).

The Alexandra Fjord highland study site was a polar desert located on the western plateau (ca. 500 m a.s.l.) approximately 5 km to the southwest of Alexandra Fjord lowland. The highlands of Alexandra Fjord are within the Churchill Structural Province of the Canadian Shield Geological Region (Batten and Svoboda 1994). Upland soils are predominantly Regosolic Turbic Cryosols with both granitic and dolomitic parent materials. Air temperature in the upland tends to be cooler than the central area of the lowland, though the mean monthly air temperature in July (4.4°C) is comparable (Labine 1994). The upland has only 40% of the vascular species found in the

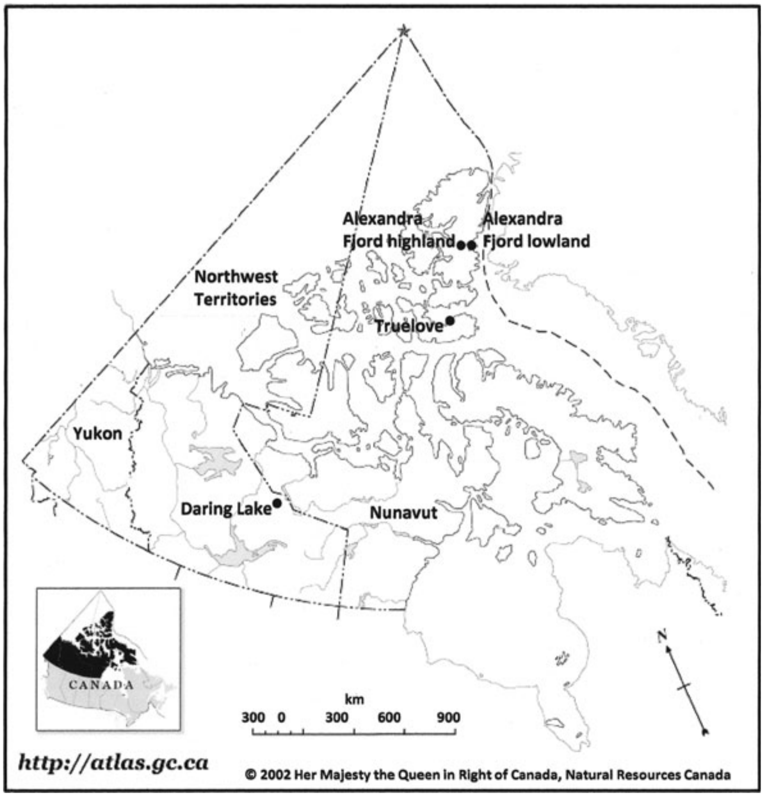

Fig. 1 Location of study sites in the Canadian high and low arctic. High arctic sites were at Alexandra Fjord highland and lowland, Ellesmere Island Nunavut Territory and at Truelove Lowlands, Devon Island, Nunavut Territory. The low arctic site was at Daring Lake, Northwest Territories

lowland. Polygonal ground creates microrelief in the polar desert that impacts the distribution of plant species (Batten and Svoboda 1994). Transects were placed over relatively flat terrain with some polygons present. *Saxifraga oppositifolia-Luzula*, *Salix arctica-Cassiope tetragona* Dwarf-shrub, *Dryas*-barrens and *Dryas-Carex* complex were the dominant plant communities along the transects (follows Batten and Svoboda 1994).

The Truelove Lowland site was located in a 43 km^2 lowland oasis on Devon Island. The lowland was bordered by shoreline to the north, west and part of the south and by steep cliffs (ca. 300 m) to the east and remaining south (Bliss 1987). Pleistocene age deposits that overlay a Precambrian complex of granulites and granitic gneisses are present. Soils were predominately Regosolic Static Cryosols and better-developed Brunisolic Eutric Static Cryosols. Average air temperature is −16 to −19°C with summer temperatures averaging 3 to 6°C (Bliss et al. 1994). Mean annual precipitation in the area ranges from 150 to 200 mm with approximately 36 mm of precipitation at Truelove during the summer. Transects were placed over a series of beach ridges. Ridges were dominated by Cushion plant—lichen communities and the intervening lowlands by Hummocky sedge-moss meadows (follows Muc and Bliss 1987).

The Daring Lake study site was located at the Tundra Ecosystem Research Station, Northwest Territories. The site was in a low arctic tundra region within the physiographic zone of the Bear-Slave Upland of the Canadian Shield, approximately 90 km northeast of the northern limit of continuous trees (Obst 2008). Elevation ranges from 414–470 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. Soils were predominately Orthic Dystric Turbic Cryosols with well-drained sand and unsorted gravel sub-soils with shallow (<0.03 m) organic layers on upper esker slopes (Lafleur and Humphreys, 2008). Average air temperature is −10.5°C and mean monthly air temperature in July is +13°C (Obst 2008). Transects were placed perpendicular to an east-west oriented esker with sample plots in upper slope areas predominately in Xerophytic Herb Tundra and Heath-Lichen Tundra, back slope plots in Heath-Mat Tundra and Birch Hummock and lower slope plots in Birch Hummock and Sedge Meadows (follows Obst 2008).

Transect sampling

At Alexandra Fjord, samples were collected at 31 points (0, 0.1, 0.2, 0.5,1, 2, 5, 10, 20, 50, 100, 100.1, 100.2, 100.5, 101, 102, 105, 110, 120, 150, 200, 200.1, 200.2, 200.5, 201, 202, 205, 210, 220, 250, 300 m) along three parallel transects 2 m apart for a total of 93 samples. In the Alexandra Fjord lowland, the transects were perpendicular to the slope of the lowland. In the Alexandra Fjord highland polar desert, transects were positioned such that the first 100 m were in the dolomitic desert and the remainder was in granitic desert. At Truelove lowland, samples were collected at 128 points located every 2 m on a 256 m transect. This transect crossed two raised beach crests and thus, captured the majority of the soil types present at Truelove, Raised Beach Crest, Upper Fore Slope, Lower Fore Slope and Sedge Meadow. At Daring Lake three parallel transects 2 m apart were placed perpendicular to an east-west oriented esker. Samples were collected at 34 points on each transect including upslope (0, 0.1, 0.2, 0.5,1, 2, 5, 10, 15, 20 m), back slope (0, 0.1, 0.2, 0.5,1, 2, 5, 10, 15, 20 m) and lower slope (0, 0.1, 0.2, 0.5,1, 2, 5, 10, 15, 20, 40, 60, 80, 100 m) positions for a total of 102 samples. A GPS unit (Trimble^{TM} GPS Systems, California, USA) was used to identify spacing (+/− 8 cm) between samples.

Vascular plant and cryptogam functional composition was assessed in 0.5 m by 0.5 m quadrats at each sampling point. The percent cover of each vascular species was assessed individually by eye as was the total cover of bryophytes and lichens and bare ground (rocks, gravel, and finer materials). A surface sample (19 cm^2, 1 cm depth) for N_2-fixation measurement was collected from within each quadrat. The surface samples selected were as representative as possible of the dominant vegetation functional groups and N_2-fixing associations within each quadrat. Due to the scale and focus of our study detailed composition of individual surface samples was not determined. However, samples had varying compositions of N_2-fixing and non-fixing lichen species, mosses, liverworts, hornworts, vascular plant stems, leaf litter, soil crusts, bare soil and sand. A soil sample of approximately 10 cm depth was collected directly below each N_2-fixation surface sample and gravimetric moisture was determined.

N_2-fixation rates

Surface samples from high arctic sites including Alexandra Fjord lowland, Alexandra Fjord highland and Truelove (July 2008) were collected at each transect position. Samples were kept cool (~4°C) and shipped to the laboratory at the University of Northern British Columbia.

Measurements of N_2-fixation were made using acetylene reduction assays (ARA) (Stewart et al. 1967). Acetylene gas (C_2H_2) was generated from CaC_2 and water, with incubations injected with 10% (*v*/*v*) acetylene. Ethylene concentrations were measured 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.

High arctic surface samples (19cm^2, 1 cm depth) from each transect position were given a wetting pretreatment at optimal hydration levels in a growth chamber for 72 h under a 17/7 h light (200 μmol PAR $m^{-2}s^{-1}$)/dark cycle with temperatures at 15°C during light hours and 5°C during dark hours. Samples were then enclosed in 250 ml glass canning jars with modified lids containing a rubber septum and 6 h ARAs were conducted under optimal environmental conditions (200 μmol PAR $m^{-2}s^{-1}$, 20°C). For each of our samples several different cyanobacterial species may have been present, each with varying optimal operating environments. However, for several species/environments an optimal temperature of ~20°C (Basilier and Granhall 1978; Chapin et al. 1991; Liengen 1999) and light saturation at ~100 μmol PAR $m^{-2}s^{-1}$ (Coxson and Kershaw 1983; Chapin et al. 1991) have been demonstrated.

Surface samples at Daring Lake were collected and incubated in the field (August 20th–30th, 2008) under the same optimal environmental conditions following the same procedure with the exception of an 24 h wetting pretreatment since samples were already hydrated due to concurrent precipitation events. Photosynthetically Active Radiation (PAR) and temperature in incubation chambers were monitored every 30 min during ARA incubations. In the laboratory the environmental chamber was adjusted as necessary to maintain optimal conditions in the incubation chambers and in the field incubation chambers were placed in water baths and bath temperature was altered.

To determine if the shipping of surface samples had a significant detrimental effect on the N_2-fixation rates detected we re-sampled the Alexandra Fjord highland transects in situ on July 11th–15th 2009. Samples were treated and ARAs were conducted in the same manner as those at Daring Lake in 2008. N_2-fixation rates at Alexandra Fjord highland were higher for samples incubated in the field in 2009 than after shipping in 2008 (72 and 49 μmol C_2H_2 reduced $m^{-2}h^{-1}$ respectively), however, the difference was not significant (*t*-test,, $t=-3.12$, df=181, $p=0.05$ for data analyzed in log units).

Statistics

We used multi-group Structural Equation Modeling (SEM) with observed variables to separate the direct and indirect effects of soil moisture, plant community functional composition, and potential N_2-fixing association abundance on rates of nitrogen fixation. SEM allows the direct and indirect theoretical causal relationships between a series of intercorrelated variables to be tested (Shipley 2000; Grace 2006). In a SEM figure each single-headed arrow represents a causal relationship such that the variable at the tail of the arrow is believed to be a direct cause of the variable at the head, while a double-headed arrow indicates an unresolved correlation between two variables. An initial SEM is specified based on prior theoretical knowledge, and is then tested to determine whether the covariance structures implied by the model adequately fit the actual covariance structures of the data. An initial theory-based model that adequately fits the data is a powerful confirmation of the validity of the theory used to construct the initial model. If the initial model does not adequately fit the data then model modification indices provide a strong tool for data exploration and hypothesis generation (Grace 2006). In a multi-group SEM the same initial path model is fit to each group (in this case study site) with all model parameters constrained to be equal between groups. Model fitting involved the progressive relaxation of parameter constraints allowing particular parameters to differ between two or more groups. The identification of cases where parameter values differ between groups is an indication that the process represented by that path coefficient is operating differently at each site.

The initial structural equation model (Fig. 2) was developed to describe how the effects of vascular plant community functional composition on bryophyte and lichen abundance indirectly influence N_2-fixation. The continuous variables included in the model are described in Online Resource 1. Vascular plant functional composition was incorporated into the model by separating the total% cover of vascular plants into shrubs, gramminoids, and forbs. Due to strong differences in plant communities between sites there was little overlap in species composition between sites and thus a more detailed classification of functional types was not possible. Direct paths from potential N_2-fixing cyanobacteria associations (Bryophyte, Lichen and Bare ground) to N_2-fixation were included. Bare ground was included as a potential N_2-fixing association because BSCs, which are communities composed of bacteria, cyanobacteria, algae, mosses, liverworts, fungi and small lichens, were not explicitly included and where present would have been recorded as bare ground. Each of the potential N_2-fixing associations received a direct path from each of the plant community functional groups (Shrubs, Gramminoids and Forbs) and Bryophytes, Lichens, Shrubs, Gramminoids and Forbs all received a direct path from Soil Moisture. The interactions between plant communities and environmental factors such as soil moisture can be important in determining both the ability of N_2-fixers to survive and the rates at which they can fix N_2. Soil moisture is a key environmental factor determining the distribution of vegetation types in arctic environments (Oberbauer and Dawson 1992) and vegetation functional types can play a major role in determining the operating environment of N_2-fixing associations (Zielke et al. 2002; 2005).

The SEM models were fit using Amos 17.0 (Amos Development Corporation, Crawfordville, FL, USA). An initial multigroup SEM was fit with all model parameters constrained to be equal between sites. This model did not have adequate fit ($\chi_{113}^2=2750.703$, $p<0.0001$). Parameter constraints were progressively

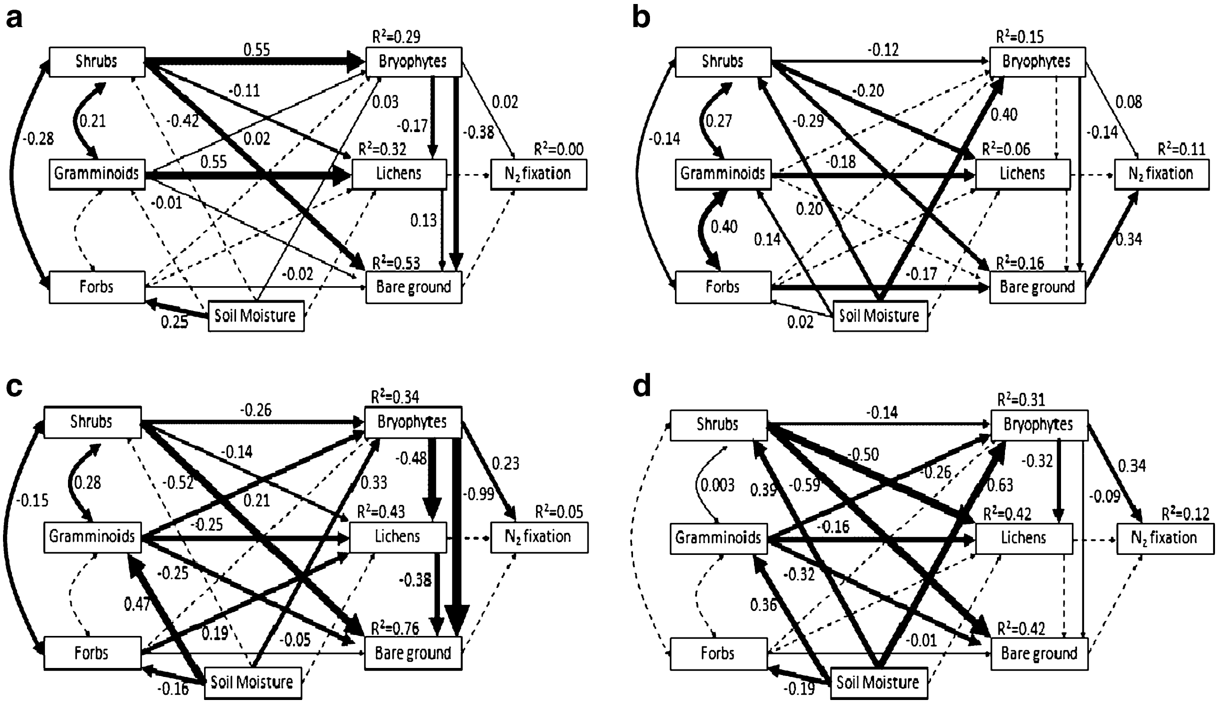

Fig. 2 Final structural equation models for **a** Alexandra Fjord highland, Ellesmere Island NT **b** Alexandra Fjord lowland, Ellesmere Island NT, **c** Truelove Lowlands, Devon Island NT and **d** Daring Lake, NWT. Significant paths are indicated by solid arrows of varying thickness that reflect the magnitude of the standardized SEM coefficients given beside each path. Nonsignificant paths are indicated by dotted arrows

relaxed in subsequent models with a drop in the CMIN statistic (Grace 2006) used as justification to retain a new model. The parameter constraint to relax in each model was selected based on examination of the matrix of standardized residuals for large values. Model fitting continued until an adequate χ^2 test was achieved (final model $\chi_{59}{}^2$=54.235, p=0.651).

Results

The final model adequately fit these data ($\chi_{59}{}^2$= 54.235, p=0.651), and explained 0, 11, 5 and 12% of the variation in N_2-fixation at the Alexandra Fjord highland, Alexandra Fjord lowland, Truelove and Daring Lake sites respectively (Fig. 2). Unstandardized path coefficients, *t*-test results and total direct and indirect effects are summarized in Online Resource 1. Despite the low r^2 values the SEM revealed important and consistent patterns of N_2-fixation across the Arctic. The zero r^2 value for N_2-fixation at Alexandra Fjord highland indicates that, with the exception of a very small contribution from bryophytes, several other important factors controlling fixation at this site are missing from the model. Increasing soil moisture was strongly associated with an increasing presence of bryophytes and increasing bryophyte abundance was a major factor determining higher N_2-fixation rates at all arctic sites (Fig. 2). Standardized path coefficients for the bryophyte –N_2-fixation relationship varied between sites, however the unstandardized coefficient was the same for all high arctic sites, indicating that the bryophyte –N_2-fixation relationship is likely consistent across the entire Arctic. Surprisingly lichen abundance had no effect on rates of N_2-fixation at any of the sites. Bare ground had a positive influence on N_2-fixation at Alexandra Fjord lowland (0.34), but bare ground had no effect on N_2-fixation at the other sites.

Mean percent cover of vegetation functional groups and mean acetylene reduction rates varied between sties (Table 1). The relationships between soil moisture and vascular plant community functional groups also varied between sites, but the influence of soil moisture on bryophyte and lichen abundance was consistent. At all sites increasing soil moisture had a direct positive effect on bryophyte abundance (0.03 Alexandra Fjord highland; 0.40 Alexandra Fjord lowland; 0.33 Truelove; 0.63 Daring Lake), while soil moisture had no effect on lichen abundance at any of the sites. In fact, there was no soil moisture, lichen and N_2-fixation pathway at any of the sites.

Increasing soil moisture appears to directly promote bryophyte abundance, however, at sites such as Alexandra Fjord lowland (0.20) and Daring Lake (0.39) where higher soil moisture also promotes shrub abundance, soil moisture had indirect negative effects on bryophyte abundance (−0.02 and −0.15 respectively) (Online Resource 1). With the exception of the Alexandra Fjord highland site, we found consistent negative effects of the vascular plant community on N_2-fixing association abundance that suggest exclusion of N_2-fixers. Higher shrub abundance had a direct negative influence on bryophyte and lichen abundance at all sites, except at Alexandra Fjord highland where bryophyte abundance was increased (0.55). Similarly, increasing gramminoids abundance led to lower abundance of lichens at all sites, except Alexandra Fjord highland where lichen abundance was higher.

Discussion

Our model revealed a strong and consistent relationship of increasing soil moisture positively influencing bryophyte abundance and increasing bryophyte abundance positively influencing N_2-fixation rates across the Canadian Arctic.

The direct and indirect influences of soil moisture are perhaps the most important factors in structuring plant species distribution at a local level within arctic landscapes (Webber 1978; Bliss 1987; Walker et al. 1989; Bliss et al. 1994; Oberbauer and Dawson 1992; Gold and Bliss 1995b). Due to a lack of roots, bryophytes and lichens are often considered to be less tightly associated with soil properties than vascular plants. While soil moisture did not have a significant influence on lichen abundance at any of our sites, soil moisture does appear to have an important influence on bryophyte abundance. Lichens are often established on drier exposed habitats and due to their sensitivity to desiccation N_2-fixation by lichens is often tightly coupled with precipitation events (Crittenden and Kershaw 1979). Patches of bryophytes, however, are often associated with permanent desiccation cracks and/or microtopographical depressions in the landscape where soil moisture content is higher (Sohlberg

Table 1 Mean percent cover of vegetation functional groups and mean acetylene reduction rates at Alexandra Fjord highland, Ellesmere Island NT, Alexandra Fjord lowland, Ellesmere Island NT, Truelove Lowlands, Devon Island NT and Daring Lake, NWT. Values are means with standard error

Site	Mean% Cover						Mean Acetylene Reduced (μmol m^{-2}h^{-1})
	Shrubs	Gramminoids	Forbs	Bryophytes	Lichens	Bareground	
Alexandra Fjord highland	13 (1.2)	0.3 (0.04)	1.6 (0.25)	6.0 (0.95)	24 (1.6)	73 (2.7)	49 (9.6)
Alexandra Fjord lowland	39 (1.3)	5.5 (0.63)	3.5 (0.48)	21 (1.7)	8.1 (0.93)	2.6 (0.58)	18 (3.2)
Truelove lowland	21 (1.2)	11 (1.1)	6.0 (0.35)	43 (2.1)	23 (1.3)	16 (1.6)	12 (1.4)
Daring Lake	53 (3.5)	15 (1.8)	0.17 (0.085)	34 (3.5)	43 (3.0)	7.9 (2.0)	31 (6.6)

and Bliss 1984). In addition, bryophytes tend to form thick mats that can hold water and nutrients from snowflush runoff or precipitation and remain moist throughout the growing season due to reduced soil evaporation (Bliss and Gold 1994; Gold and Bliss 1995b). Even with limited precipitation inputs high soil moisture can be maintained by the upward wicking of permafrost meltwater from the thaw front at the base of the active layer.

Moisture can directly affect rates of N_2-fixation within individual N_2-fixing communities (Chapin et al. 1991; Chapin and Bledsoe 1992; Nash and Olafsen 1995; Zielke et al. 2002, 2005; Gundale et al. 2009). However, our study focused upon the indirect effects of moisture on N_2-fixation in order to better understand relationships between vegetation functional types and N_2-fixation across the Canadian Arctic. Spatial heterogeneity in N_2-fixation is often a reflection of differences in cyanobacterial biomass due to the long-term characteristics of the community moisture regime (Chapin et al. 1991). Cyanobacteria are often closely associated with bryophytes where moisture conditions are more favourable (Alexander et al. 1978; Arndal et al. 2009) and the cyanobiont may receive carbohydrates from the host (Turetsky 2003). The dense packing of stems and leaves provides protection from desiccation and enables water translocation to the cyanobacterial zone (Line 1992). Gundale et al. 2009 found a feathermoss-cyanobacterial association had an increased N_2-fixation capacity after 45 days of persistent moisture. Although the precise mechanism for this increased capacity remains undetermined, it may involve changes in cyanobacterial population size, community composition, dormancy or altered physiological efficiency of the association. Moisture enhances the metabolic activity of N_2-fixing associations by increasing carbon and energy supplies for N_2-fixation and by stimulating net primary production (Wierenga et al. 1987; Hartley and Schlesinger 2002).

The direct influence of water availability as a limiting factor and determinant of vegetation structure, productivity and composition, declines with decreasing latitude from high to low Arctic (Oberbauer and Dawson 1992). We found soil moisture played an important role in both high arctic polar oases and in the low Arctic; where higher soil moisture led to a higher abundance of vascular plant types, such as shrubs. Shrubs however had a negative effect on bryophyte abundance at all sites with the exception of Alexandra Fjord highland, where both shrubs and gramminoids had a positive influence. At Daring Lake in the low Arctic both shrubs and gramminoids had a negative effect on bryophyte abundance. Therefore, the importance of competition from vascular plants, potentially through shading, may increase at lower latitudes. Nitrogen fixation tends to decrease with increasing vegetation development, advancing succession and increasing plant cover (Crocker and Major 1955; Liengen and Olsen 1997; Sorensen et al. 2006).

In warming experiments a stronger vegetative growth response has been observed in the low Arctic, whereas, in colder high arctic sites a greater reproductive response associated colonization of unvegetated ground may occur (Arft et al. 1999). It has been suggested that declining macrolichen abundance in warming sub- and mid-arctic environments may be a function of increased growth and abundance of shrubs, which may inhibit lichen performance through shading (Cornelissen et al. 2001). Rates of N_2-fixation and persistence of other N_2-fixing associations such as bryophyte-cyanobacterial associations may be similarly influenced by reduced light availability. Lower rates of N_2-fixation with increasing shrub cover may also occur due to higher N availability and turnover under shrub canopies, which in turn may down-regulate N_2-fixation (Zackrisson et al. 2004; DeLuca et al. 2007). N_2-fixation by shrub species themselves may also lead to reduced N_2-fixation rates by bryophyte-cyanobacterial associations. While N_2-fixing shrubs are relatively rare at in the Arctic, *Dryas integrifolia* Vahl., which is known to fix N_2 (Henry and Svoboda 1986), was found at all sites except Daring Lake.

Polar deserts are particularly important considering most of the ice-free terrestrial environments within the Canadian High Arctic are polar desert (44%) or semidesert (49%) (Bliss and Gold 1999). The positive relationships between shrubs, gramminoids and bryophytes found only at Alexandra Fjord highland likely reflects the influence of an extreme polar desert environment where abiotic factors play a more important role in structuring vegetation distribution. Polar deserts tend to have a patchy distribution of the most productive areas with desiccation-cracks, the margins of soil polygons and stripes and other slight concavities being important sites for seed germination and seedling establishment (Sohlberg and Bliss 1984; Bliss and Gold 1994; Gold and Bliss 1995b). Vascular plant cover and succession in polar deserts appears to be tightly linked to these sites where a greater cover of cryptogams is also found (Bliss et al. 1994; Dickson 2000; Breen and Lévesque 2008). These microsites tend to have higher temperature, lower wind speeds, greater soil moisture and higher nitrate levels (Sohlberg and Bliss 1984). Some vascular plant species may promote N_2-fixation by increasing the bioavailability of other elements that are necessary for N_2-fixation, such as phosphorus. For example, higher concentrations of bioavailable P and higher rates of N_2-fixation in feathermoss-cyanobacterial communities have been observed under juniper canopies compared with open heath tundra (DeLuca and Zackrisson 2007). Vegetation in polar deserts appears to be distributed by their abiotic tolerances with no evidence of incipient niche differentiation and no competitive exclusion of species from vegetated sites (Sohlberg and Bliss 1984).

Nitrogen supplied through cyanobacterial N_2-fixation is the only significant source in polar desert communities with total soil N below well-developed cryptogamic crusts (0.09%) doubling that of non-crusted sites (0.04%) (Gold and Bliss 1995b). Therefore, it is not surprising that we found a higher mean rate of N_2-fixation at Alexandra Fjord highland compared to the other sites (Table 1). Zackrisson et al. 2009 also found N_2-fixation rates in moss-cyanobacterial associations were generally low at southern latitudes and higher at northern latitudes (64–69°C). Climatic changes may directly affect N_2-fixation rates as a result of warmer temperatures and changes in moisture availability, however as our study suggests N_2-fixation may also be indirectly affect by alterations in the distribution and abundance of vegetation types. Many of these changes however, will differ depending on both latitude and site-to-site variability.

The low r^2 values in this study indicate that while soil moisture is clearly a significant driver of N_2-fixation, there are other important factors that affect N_2-fixation in arctic systems that were not included in the model. The aggregate of these missing factors are likely to be much stronger drivers of N_2-fixation than variation in soil moisture alone. The colonization frequencies, abundance, and distribution of N_2-fixing organisms and/or rates of N_2-fixation in arctic landscapes can be affected by microtopography (Schell and Alexander 1973; Henry and Svoboda 1986), microaspect (George et al. 2000; Davidson et al. 2002), soil texture (Kleiner and Harper 1977; Anderson et al. 1982; Verrecchia et al. 1995; Harper and Belnap 2001; Gold et al. 2001), soil pH (Ponzetti and McCune 2001; Smith et al. 2002; Turetsky 2003), nutrient availability (Chapin and Bledsoe 1992; Vitousek et al. 2002; Zackrisson et al. 2009), successional age (DeLuca et al. 2007; Lagerström et al. 2007; Zackrisson et al. 2004), surface moisture (Dickson 2000; Breen and Lévesque 2008) and disturbance history (Belnap 2002). Since N_2-fixation occurs in response to this large suite of intercorrelated variables inclusion of additional factors would likely increase r^2 values. In addition, a more detailed identification of N_2-fixing associations present would have also likely increased the explanatory power of our model. For example, lichen cover included both N_2-fixing and non-fixing lichens and bare soil included both BSCs and uncolonized soil. In our relatively simple model the importance of bryophytes in N_2-fixation across the Canadian Arctic is evident. Our findings suggest that a moisture-bryophyte-N_2-fixation relationship is found across the Canadian Arctic in many different vegetation types and at different latitudes. Given the importance of bryophyte N to gross ecosystem productivity the role of bryophytes in arctic nutrient availability needs to be further explored, especially in the light of climatic changes currently occurring across the Arctic.

Acknowledgements We thank Ian Snape, Greg Henry, Alanna DeBusschere and Rebecca Carmichael for assistance in the field and lab. This study was supported by the International Polar Year 2007–2008 in collaboration with Climate Change Impacts on Canadian Arctic Tundra (CiCAT) project and an NSERC post-doctoral fellowship to E.G.L.

References

Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD, Jonsdottir IS, Laine K, Levesque E, Marion GM, Molau U, Molgaard P, Nordenhall U, Raszhivin V, Robinson CH, Starr G, Stenstrom A, Stenstrom M, Totland O, Turner PL, Walker LJ, Webber PJ, Welker JM, Wookey PA (1999) Responses of tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. Ecol Monogr 69:491–511

Alexander V, Schell DM (1973) Seasonal and spatial variation of nitrogen fixation in the Barrow, Alaska, Tundra. Arct Alp Res 5:77–88

Alexander V (1974) A syntheses of the IBP tundra biome circumpolar study of nitrogen fixation. In: Holding AJ, Heal OW, MacLean SF, Flanagan PW (eds) Soil Organisms and Decomposition in Tundra. Biome Steering Committee, Stockholm, pp 109–121

Alexander VM, Billington M, Schell DM (1978) Nitrogen fixation in arctic and alpine tundra. In: Tieszen LL (ed) Vegetation and Production Ecology of an Alaskan Arctic Tundra. Springer, New York, pp 539–558

Anderson DC, Harper KT, Holmgren RC (1982) Factors influencing development of cryptogamic soil crusts in Utah deserts. J Range Manag 35:180–185

Arndal MF, Illeris L, Michelsen A, Albert K, Tamstorf M, Hansen BU (2009) Seasonal variation in gross ecosystem production, plant biomass, and carbon and nitrogen pools in five high arctic vegetation types. Arct Antarct Alp Res 41:164–173

Basilier K, Granhall U (1978) Nitrogen fixation in wet minerotrophic moss communities of a subarctic mire. Oikos 31:236–246

Batten DS, Svoboda J (1994) Plant communities on the uplands in the vicinity of the Alexandra Fiord Lowland. In: Svoboda J, Freedman B (eds) Ecology of a Polar Oasis: Alexandra Fiord Ellesmere Island. Captus University Publications, Toronto, pp 97–112

Belnap J, Büdel B, Lange OL (2001) Biological soil crusts: Characteristics and distribution. In: Belnap J, Lange OL (eds) Biological Soil Crusts: Structure, Function, and Management. Springer, New York, pp 3–30

Belnap J (2002) Nitrogen fixation in biological soil crusts from southeast Utah, USA. Biol Fertil Soils 35:128–135

Bliss LC (1987) Truelove Lowland. A high arctic ecosystem. University of Alberta Press, Edmonton Devon Island, Canada

Bliss LC, Gold WG (1994) The patterning of plant communities and edaphic factors along a high arctic coastline: Implications for succession. Can J Bot 72:1095–1107

Bliss LC, Henry GHR, Svoboda J, Bliss DI (1994) Patterns of plant distribution within two polar desert landscapes. Arct Alpin Res 26:46–55

Bliss LC, Gold WG (1999) Vascular plant reproduction, establishment, and growth and the effects of cryptogamic crusts within a polar desert ecosystem, Devon Island, N.W. T., Canada. Can J Bot 77:623–636

Breen K, Lévesque E (2008) The influence of biological soil crusts on soil characteristic along a high arctic glacier foreland, Nunavut, Canada. Arct Antarct Alp Res 40:287–297

Chapin DM, Bliss LC, Bledsoe LJ (1991) Environmental regulation of nitrogen fixation in a high arctic lowland ecosystem. Can J Bot 69:2744–2755

Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of Arctic Tundra to experimental and observed changes in climate. Ecol 76:694–711

Chapin DM, Bledsoe C (1992) Nitrogen fixation in arctic plant communities. In: Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (eds) Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective. Academic, New York, pp 301–319

Convey P, Smith RIL (2006) Responses of terrestrial Antarctic ecosystems in climate change. Plant Ecol 182:1–10

Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Jones GD, Jonasson S, Chapin FS III, Molau U, Neil C, Lee JA, Mellillo JM, Sveinbjornsson B, Aerts R (2001) Global change and arctic ecosystems: Is lichen decline a function of increases in vascular plant biomass. J Ecol 89:984–994

Coxson DS, Kershaw KA (1983) Rehydration response of nitrogenase activity in terrestrial *Nostoc commune* from Stipa-Bouteloa grassland. Can J Bot 61:2658–2668

Crittenden PD, Kershaw KA (1978) Discovering the role of lichens in the nitrogen cycle in the Boreal-Arctic ecosystem. Bryol 81:258–267

Crittenden PD, Kershaw KA (1979) Studies on lichen-dominated systems. XXII. The environmental control of nitrogenase activity in Stereocaulon paschale in spruce-lichen woodland. Can J Bot 57:236–254

Crocker RL, Major J (1955) Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J Ecol 43:425–448

Davey A (1983) Effects of abiotic factors on nitrogen fixation by blue-green algae in Antarctica. Polar Biol 2:95–100

Davidson DW, Bowker M, George D, Philips SL, Belnap J (2002) Treatment effects on performance of N-fixing lichens in disturbed soil crusts of the Colorado plateau. Ecol Appl 12:1391–1405

DeLuca TH, Zackrisson O, Nilsson M-C, Sellstedt A (2002) Quantifying nitrogen-fixation in feather moss carpets of boreal forests. Nature 419:917–920

DeLuca TH, Zackrisson O (2007) Enhanced soil fertility under *Juniperus communis* in arctic ecosystems. Plant Soil 294:157–155

DeLuca TH, Zackrisson O, Francesco G, Sellstedt A, Nilsson M-C (2007) Ecosystem controls on nitrogen fixation in boreal feather moss communities. Oecologia 152:121–130

Dickson LG (2000) Constraints to nitrogen fixation by cryptogamic crusts in a polar desert ecosystem, Devon Island, N.W.T., Canada. Arct Alp Res 32:40–45

Foster DR (1985) Vegetation development following fire in *Picea mariana* (black spruce)-*Pleurozium* forest of south-eastern Labrador, Canada. J Ecol 73:517–534

George DB, Davidson DW, Schleip KC, Patrell-Kim LJ (2000) Microtopography of microbiotic crusts on the Colorado Plateau, and the distribution of component organisms. West N Am Nat 60:343–354

Goetz SJ, Bunn AJ, Fiske GJ, Houghton RA (2005) Satellite observed photosynthetic trends across boreal North America associated with climate and fire disturbance. Proc National Acad of Sci 102:13521–13525

Gold WG, Glew KA, Dickson LG (2001) Functional influences of cryptobiotic surface crusts in an alpine tundra basin of the Olympic Mountains, Washington, U.S.A. Northwest Sci 75:315–326

Gold WG, Bliss LC (1995a) The nature of water limitations for plants in a high arctic polar desert. In: Callaghan T (ed) Global Change and Arctic Terrestrial Ecosystems. European Commission, Luxembourg, pp 149–155

Gold WG, Bliss LC (1995b) Water limitations and plant community development in a high arctic polar desert. Ecol 76:1558–1568

Grace JB (2006) Structural Equation Modeling and Natural Systems. Cambridge University Press, Cambridge

Granhall U, Lid-Torsvik V (1975) Nitrogen fixation by bacteria and free-living blue-green algae in tundra areas. In: Wielgolaske FE (ed) Fennoscandian Tundra Ecosystems, part 1. Springer, New York, pp 306–315

Gundale MJ, Gustafsson H, Nilsson M-C (2009) The sensitivity of nitrogen fixation by a feathermoss-cyanobacteria association to litter and moisture variability in young and old boreal forests. Can J For Res 39:2542–2549

Gunther AJ (1989) Nitrogen fixation by lichens in a subarctic Alaskan watershed. Bryol 92:202–208

Harper KT, Belnap J (2001) The influence of biological soil crusts on mineral uptake by associated vascular plants. J Arid Environ 47:347–357

Hartley AE, Schlesinger WH (2002) Potential environmental controls on nitrogenase activity in biological crusts of northern Chihuahuan Desert. J Arid Environ 52:293–304

Henry GHR, Svoboda J (1986) Dinitrogen fixation (acetylene reduction) in high arctic sedge meadow communities. Arct Antarct Alp Res 18:181–187

Hobara S, McCalley C, Koba K, Giblin AE, Weiss MS, Gettel GM, Shaver GR (2006) Nitrogen fixation in surface soils and vegetation in an Arctic tundra watershed: A key source of atmospheric nitrogen. Arct Antarct Alp Res 38:363–372

Houle D, Bilodeau Gauthier S, Paquet S, Planas D, Warren A (2006) Identification of two genera of N_2-fixing cyanobacteria growing on three feather moss species in boreal forest of Quebec, Canada. Can J Bot 84:1025–1029

Kallio S, Kallio P (1975) Nitrogen fixation in lichens at Kevo, North Finland. In: Wielgolaske FE (ed) Fennoscandian Tundra Ecosystems, part 1. Springer, New York, pp 292–304

Kershaw KA (1976) Studies on lichen-dominated systems. XX An examination of some aspects of the northern boreal lichen woodlands in Canada. Can J Bot 55:393–410

Kleiner EF, Harper KT (1977) Soil properties in relation to cryptogamic groundcover in Canyonlands National Park. J Range Manag 30:202–205

Kurina LM, Vitousek PM (1999) Controls over the accumulation and decline of a nitrogen-fixing lichen, *Stereocaulon vulcani*, on young Hawaiian lava flows. J Ecol 87:784–799

Labine C (1994) Meteorology and climatology of the Alexandra Fiord Lowland. In: Svoboda J, Freedman B (eds) Ecology of a Polar Oasis: Alexandra Fiord Ellesmere Island. Captus University Publications, Toronto, pp 23–40

Lafleur PM, Humphreys ER (2008) Spring warming and carbon dioxide exchange over low arctic tundra in central Canada. Glob Chang Biol 14:1–17

Lagerström A, Nilsson MC, Zackrisson O, Wardle DA (2007) Ecosystem input of nitrogen through biological fixation in feather mosses during ecosystem retrogression. Funct Ecol 21:1027–1033

Liengen T, Olsen RA (1997) Seasonal and site-specific variations in nitrogen fixation in a high Arctic area, Ny-Alesund, Spitsbergen. Can J Microbiol 43:759–769

Liengen T (1999) Environmental factors influencing the nitrogen fixation activity of free-living terrestrial cyanobacteria from a high arctic area, Spitsberg. Can J Microbiol 45:573–581

Line MA (1992) Nitrogen fixation in the sub-Antarctic Macquarie Island. Polar Biol 11:601–606

Muc M, Bliss LC (1987) Plant communities of Truelove Lowland. In: Bliss LC (ed) Truelove Lowland, Devon Island, Canada: A high arctic ecosystem. University of Alberta Press, Edmonton, pp 143–154

Muc M, Freedman B, Svoboda J (1989) Vascular plant communities of a polar oasis at Alexandra Fiord (79^{o}N), Ellesmere Island, Canada. Can J Bot 67:1126–1136

Nash TH III, Olafsen AG (1995) Climate change and the ecophysiological response of Arctic lichens. Lichenol 27:559–565

Oberbauer SF, Dawson TE (1992) Water relations of arctic vascular plants. In: Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J (eds) Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective. Academic, New York, pp 259–275

Obst J (2008) Classification of land cover, vegetation communities, ecosystems and habitats in East Daring Lake Basin, Northwest Territories. Prepared for Department of Environment and Natural Resources, Wildlife Division Government of the Northwest Territories and Environment and

Conservation Division. Indian and Northern Affairs Canada, Yellowknife, NT

Ponzetti JM, McCune BP (2001) Biotic soil crusts of Oregon's shrub steppe: Community composition in relation to soil chemistry, climate, and livestock activity. Bryol 104:212–225

Schell DM, Alexander V (1973) Nitrogen fixation in Arctic coastal tundra in relation to vegetation and micro-Relief. Arct 26:130–137

Shipley B (2000) Cause and Correlation in Biology. Cambridge University Press, Cambridge

Smith JL, Halvorson JJ, Bolton H Jr (2002) Soil properties and microbial activity across a 500 m elevation gradient in a semi-arid environment. Soil Biol Biochem 34:1749–1757

Sohlberg EH, Bliss LC (1984) Microscale pattern of vascular plant distribution in two high arctic plant communities. Can J Bot 62:2033–2042

Soil Classification Working Group (1998) The Canadian System of Soil Classification. 3rd ed. Agric. and Agri-Food Can. Publ. 1646, Ottawa, pp. 187.

Solheim B, Endal A, Vigstad H (1996) Nitrogen fixation in Arctic vegetation and soils from Svalbard, Norway. Polar Biology 16:35–40

Solheim B, Zielke M, Bjerke JW, Rozema J (2006) Effects of enhanced UV-B radiation on nitrogen fixation in arctic ecosystems. Plant Ecol 182:109–118

Sorensen PL, Jonasson S, Michelsen A (2006) Nitrogen fixation, denitrification, and ecosystem nitrogen pools in relation to vegetation development in the subarctic. Arct, Antarct Alp Res 38:263–272

Stewart WDP, Fritzgerald GP, Burris RH (1967) *In situ* studies on N_2 fixation using the acetylene reduction technique. Proceed Natl Acad Sci USA 58:2071–2078

Sturm M, Racine C, Tape K (2001) Climate change—Increasing shrub abundance in the Arctic. Nature 411:546–547

Turetsky MR (2003) The role of bryophytes in carbon and nitrogen cycling. Bryol 106:395–409

Verrecchia E, Yair A, Kidron GW, Verrecchia K (1995) Physical properties of the psammophile crptogamic crust and their consequences to the water regime of sandy soils, north-western Negev Desert, Israel. J Arid Environ 29:427–437

Vitousek PM, Cassman K, Cleveland C, Crewes T, Field CB, Grimm NB, Howarth RW, Marino R, Martinelli L, Rastetter EB, Sprent JI (2002) Towards an ecological understanding of biological nitrogen fixation. Biogeochem 57(58):1–45

Walker DA, Binnian E, Evans BM, Lederer ND, Nordstrand E, Webber PJ (1989) Terrain, vegetation and landscape evolution of the R4D research site, Brooks Range Foothills Alaska. Holarct Ecol 12:238–261

Walker DA (2000) Hierarchical subdivision of arctic tundra based on vegetation response to climate, parent material, and topography. Glob Chang Biol 6:19–34

Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carroll AB, Epstein HE, Jonsdottir IS, Klein JA, Magnusson B, Molau U, Oberbauer SF, Rew SP, Robinson CH, Shaver GR, Suding KN, Thompson CC, Tolvanen A, Totland O, Turner PL, Tweedie CE, Webber PJ, Wookey PA (2006) Plant community responses to experimental warming across the tundra biome. Proceed Natl Acad Sci USA 103:1342–1346

Webber PJ (1978) Spatial and temporal variation of the vegetation and its production. In: Tieszen LL (ed) Vegetation and Production Ecology of an Alaskan Arctic Tundra. Springer, New York, pp 37–112

Wierenga PJ, Hendricx JM, Nash MH, Ludwig J, Daugherty LA (1987) Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. J Arid Environ 13:53–63

Zackrisson O, DeLuca TH, Nilson M-C, Selstedt A, Berglund LM (2004) Nitrogen fixation increases with successional age in boreal forests. Ecol 85:3327–3334

Zackrisson O, DeLuca TH, Gentili F, Selstedt A, Jäderland A (2009) Nitrogen fixation in mixed *Hylocomium splendens* moss communities. Oecologia 160:309–319

Zielke M, Ekker AS, Olsen RA, Spjelkavik S, Solheim B (2002) The influence of abiotic factors on biological nitrogen fixation in different types of vegetation in the high arctic, Svalbard. Arct Antarct Alp Res 34:293–299

Zielke M, Solheim B, Spjelkavik S, Olsen RA (2005) Nitrogen fixation in the high arctic: Role of vegetation and environmental conditions. Arct Antarct Alp Res 37:372–378