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Nitrogen Fixation in the High Arctic: Role of Vegetation and Environmental Conditions

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Abstract

The course of nitrogen fixation by moss-associated cyanobacteria in Svalbard (78°N, 16°E), Norway, was studied using the acetylene reduction assay. In situ field measurements of nitrogen fixation activity were conducted in six different types of moss-dominated arctic vegetation from the beginning of the snowmelt in early June to the end of July 1998. Concurrently, the water content of the soil/vegetation layer was determined and correlated with the nitrogen fixation rates. At all sites with diminishing water content during the summer season, nitrogen fixation activity was positively correlated with the amount of available water in the vegetation. At two sites, where water content of the vegetation was constantly higher than 80% (w/w) throughout the season, nitrogen fixation activity was correlated with temperature. Depending on the type of vegetation, nitrogen fixation became limited when the water status fell below a minimum threshold level. The most desiccation-tolerant vegetation for nitrogen fixation activity was the cryptobiotic crust, where nitrogen fixation decreased only after the water content of the soil/vegetation was less than 50% of the its fresh weight, while in the other types of vegetation nitrogen fixation stopped when water content was around 60%. The results from the present study confirm that, in arctic regions with low precipitation during the growing season, nitrogen fixation in different types of vegetation is mostly limited either to the period of snowmelt when water is sufficiently available, or to habitats that stay wet during summer.

Introduction

The ecosystem vegetation in the High Arctic has been defined by Bliss and Matveyeva (1992) and further subdivided by Elvebakk (1997) for Svalbard into the polar desert zone, the northern arctic zone, and the middle arctic tundra zone. The polar desert zone is sparsely vegetated, while in the middle arctic tundra zone the ground is often completely covered by plants. In all zones, primary production is limited by climatic conditions and nutrient supply (Liengen and Olsen, 1997; Dickson, 2000). With a few exceptions, such as the ornithogenic tundra, the amount of nitrogen available in the soil is one of the major factors limiting plant growth in the Arctic (Shaver and Chapin, 1980; Nadelhoffer et al., 1992). The main input of nitrogen originates from biological nitrogen fixation by cyanobacteria (Alexander, 1974; Lennihan et al., 1994; Solheim et al., 1996). Cyanobacteria are often found in great variety in all the high arctic zones, and in several ecosystems they are the dominant microorganisms in terms of biomass and productivity (Vincent, 2000). Nitrogen fixation by cyanobacteria compensates for the lack of nitrogen in arctic soils (Lennihan et al., 1994) and permits the subsequent colonization of these habitats by other microorganisms and higher plants (Bliss and Gold, 1994). Their activity depends on size and diversity of the resident cyanobacterial populations and on environmental factors. In several arctic ecosystems the vegetation is dominated by mosses harboring epiphytic cyanobacteria that contribute fixed nitrogen to the nitrogen cycle (Solheim et al., 1996; for review see Solheim and Zielke, 2002). Epiphytic associations between cyanobacteria in different species of mosses from polar regions have been studied by traditional isolation and taxonomy (Alfinito et al., 1998; Komárek, 1999), by SEM, TEM, epifluorescence, and laser confocal microscopy (Granhall and van Hofsten, 1976; Broady, 1979; Scheirer and Brasell, 1984; Scheirer and Dolan, 1983; Solheim et al., 2004), and by molecular methods (Redfield et al., 2002). These studies report a high diversity of cyanobacteria living epiphytically on moss leaves and between the stem and the leaves of a number of different mosses. Possible benefits for the cyanobacteria in this association with moss may be supply of carbohydrates and protection against desiccation and UV-radiation, whereas the moss may gain fixed nitrogen from the cyanobacteria. Although cyanobacteria are well suited for the harsh conditions in the Arctic, their activity may be limited by environmental constraints. In a previous laboratory study, Zielke et al. (2002) showed the relationship between abiotic factors such as temperature, moisture and light, and nitrogen fixation activity of epiphytic cyanobacteria from different types of vegetation in Svalbard. Considering the natural conditions in Svalbard, they concluded that the amount of available water may be the most important factor controlling nitrogen fixation. However, biotic factors may also influence cyanobacterial nitrogen fixation in arctic vegetation. Loonen and Solheim (1998) found a stimulating effect on the nitrogen fixation activity of moss-associated cyanobacteria when the vegetation was grazed by geese. These and results from other studies (Liengen, 1999; Belnap, 2001; Dickson, 2000) show that the contribution of biologically fixed nitrogen to arctic ecosystems depends strongly on climatic conditions and a range of other environmental factors.

In the present study, the ecosystem vegetation in the studied area of Spitsbergen belongs to the middle arctic tundra zone (Elvebakk, 1997), and mosses dominate in most types of vegetation (Vanderpuye, et al., 2002). Nitrogen fixation in the field during June and July was measured in habitats with different types of vegetation typically found in the polar areas (Longton, 1988). The potential for nitrogen fixation in the different vegetation types under laboratory conditions has been found to be of the same magnitude as found in situ (Zielke et al., 2002, 2003). Our hypothesis is that nitrogen fixation in high arctic vegetations with the same macroclimate will vary greatly due to different microclimate; the two main environmental factors are water and temperature.

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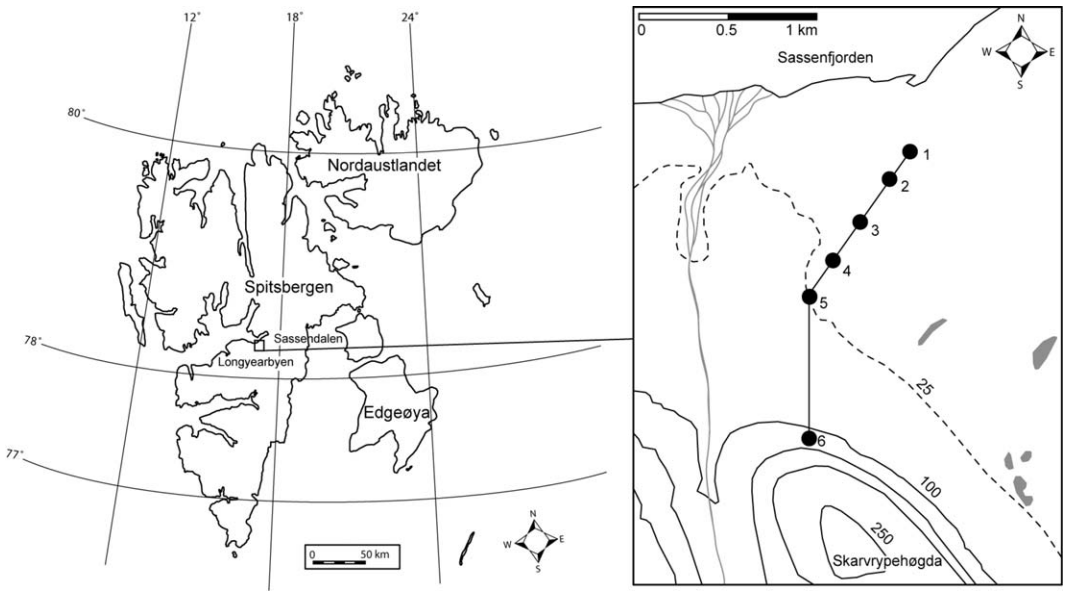

FIGURE 1. Map of the Svalbard archipelago and an overview of the location of the transect with the six study sites and the topography of the area.

In this paper we measured nitrogen fixation in the field in different types of vegetation during the first six weeks of the growing season and discuss the relationship between nitrogen fixation and water content of the soil/vegetation layer and air temperature.

Materials and Methods

SITES FOR FIELD STUDIES

The field studies were conducted along a 2-km transect in Sassendalen (78°47′N, 16°19′E) in Spitsbergen, the largest island in the Svalbard archipelago (Fig. 1). The six field sites represented different types of vegetation commonly found in the High Arctic (Elvebakk, 1994; Longton, 1988). Site 1 had more than 40% bare ground of dark silt with bead-like colonies of free-living cyanobacteria. All other sites were dominated by mosses (58–84% cover) and included a wet marsh (Site 2), a moist meadow (Site 3), a wet meadow (Site 4), a cryptogamic crust (Site 5), and a flush meadow (Site 6) (for a detailed description, see Site 1–Site 6 *in* Zielke et al., 2003; for Sassendalen, see Vanderpuye et al., 2002). Table 1 summarizes the main differences among the sites.

TABLE 1

Summary of vegetation characteristics showing main differences between sites. A more detailed description of environmental variables can be found at Zielke et al. (2003).

Site	Characteristics of the vegetation[a]
1	Sparsely vegetated salt marsh. Vascular plants (*Puccinella phryganodes* and *Carex subspathacea*) are dominating over mosses (*Sanonia uncinata*). Free-living cyanobacteria.
2	Densely covered moss dominated (*Scorpidium cossonii*) wet marsh.
3	Densely covered moss dominated (*Orthothecium chryseon*) moist meadow.
4	Densely covered wet meadow with several mosses and vascular plants (*Carex parallela*).
5	Densely covered by a cryptobiotic crust containing mosses (*Hypnum* sp.), vascular plants (*Salix polaris*), and lichens.
6	Flush meadow covered with mosses (*O. chryseon*), vascular plants (*Equisetum arvense*), lichens, and free-living cyanobacteria.

[a] Dominating moss and vascular plant species are listed in parentheses.

FIELD MEASUREMENTS

Field measurements of acetylene reduction activity were conducted during the summer of 1998. At each site five random circular soil/vegetation samples (10 cm diameter and 3 cm thickness) were cut from an area of about 10 m^2. Each individual sample was placed in a gas-tight transparent circular Perspex chamber with the same inner diameter as the sample and a total volume of 400 ml. The chambers were placed in the ground where the samples were collected and shaded from direct sunlight by a small sun-screen to avoid greenhouse effects. One control chamber with a temperature probe inside the vegetation sample and a temperature probe in the vegetation outside the chamber was included at each site for all measurements. Without shading of direct sunlight, the temperature difference between inside and outside the chamber could be more than 20°C, whereas with shading the temperature inside the chambers was only 1–2°C higher than outside. The samples were incubated in 10% (v/v) acetylene in air for 2 h. Of the gas in the chamber, 10 ml was then withdrawn through a septum with a syringe and transferred to an evacuated vial of 10 ml and stored for later analysis of ethylene concentration. A control experiment tested the vials for leaks; no leaking from the vials could be detected after two months of storage. After incubation the samples were taken out of the chambers and transferred back into the ground. All samples were repeatedly incubated from snowmelt in June every second day until 25 June. Subsequently, the samples were measured four times at approximately one week intervals until 27 July. To ascertain whether repeated incubation in acetylene influenced nitrogenase activity, additional samples from all field sites were transported to the laboratory and incubated with 10% acetylene for 2 h once per day for six days. During the six-day period, the samples were maintained at constant water content, light, and temperature. No significant changes in acetylene reduction activity could be detected. Finally, samples were incubated under laboratory conditions without acetylene to see if the

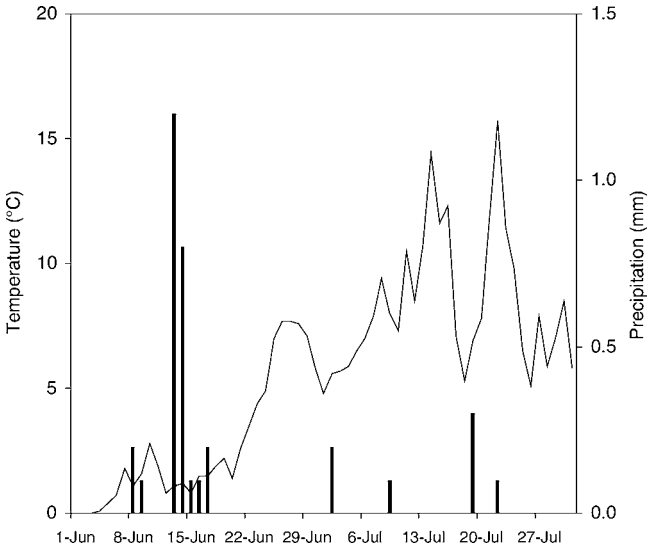

FIGURE 2. Daily mean temperatures (line) and precipitation (bars) for Longyearbyen Airport in the period of June and July 1998.

vegetation itself produced ethylene; no ethylene production could be found after 2- and 4-h incubation.

NITROGEN FIXATION MEASUREMENTS

Nitrogen fixation activity was measured using the acetylene reduction assay (Stewart et al., 1967). One mL of the gas samples from the field was analyzed for ethylene concentration on a gas chromatograph, as described previously (Zielke et al., 2002). Activity was calculated as amount of ethylene produced in μmol m^{-2} h^{-1}.

WATER CONTENT OF SAMPLES

In order to determine the water content of the soil/vegetation layer at each study site, samples of the same size as those for the nitrogen fixation measurements were taken and packed in Ziploc bags for laboratory analysis. The samples were dried in an oven at 90°C for 24 h. Since the samples were mainly composed of living and dead vegetation, water content was calculated as percent water of fresh weight of samples.

CLIMATIC CONDITIONS

Sassendalen is a valley parallel to Adventdalen. Both are situated in the inner Isfjord area approximately 40 km apart, and have a similar topography and a comparable climate; however, due to lack of precipitation data for the Sassendalen and gaps in our temperature measurements, the precipitation and temperature data from the weather station at Longyearbyen Airport are used instead. Both Longyearbyen Airport and our study area are situated at the mouth of the valleys.

STATISTICAL TREATMENT

Statistical analyses were conducted using PAST version 1.31 (http://folk.uio.no/ohammer/past/) for correlation analyses and STATISTICA 6.0 (StatSoft, Inc., www.statsoft.com, Tulsa, OK, U.S.A., 2001) for all other analyses. Normality of the data was checked using normal probability plots. To determine correlation between acetylene reduction rates and soil water content or air temperature, Pearson product-moment correlation coefficient r was calculated ($p < 0.05$). To estimate the total amount of produced ethylene at the sites during the study period, the area under the curves has been integrated. Significant differences between the means ($p \leq 0.05$) have been tested by One-way ANOVA followed by post hoc tests (Fisher's LSD).

TABLE 2

Results from analysis of correlation between acetylene reduction rates (AR) and water content of the soil/vegetation samples or air temperature.

Site	Factors	n	Period (dd/mm)	r	p
1	AR × temperature	6	19/06–11/07	0.91	<0.01
2	AR × temperature	5	17/06–25/07	0.86	<0.06
2	AR × water	4	25/06–19/07	0.99	<0.01
3	AR × temperature	5	17/06–25/06	0.89	<0.04
3	AR × water	4	25/06–19/07	0.99	<0.004
4[a]	AR × temperature	10	15/06–25/07	0.91	<0.001
5[a]	AR × temperature	3	13/06–17/06	0.99	<0.006
5	AR × water	9	13/06–11/07	0.76	<0.02
6[a]	AR × temperature	10	13/06–25/07	0.83	<0.002

[a] Correlation analysis has been performed with mean air temperatures of the day before acetylene reduction has been measured.

Results

The climate on the West Coast of Spitsbergen, represented by Adventdalen, was exceptionally dry in the summer of 1998. While the annual means of precipitation (1961–1990) for June and July are 10 and 18 mm, respectively, in 1998 only 3 and 1 mm were measured in the same two months. The mean temperatures for the study period were in the range of the annual means (1961–1990) with temperatures above freezing from June 3 (Fig. 2). The six sites became snow free in a sequence starting with Site 6 highest up in the valley side on 9 June and last at Site 1 at the bottom of the valley on 19 June. In all sites nitrogen fixation activity was detectable immediately or less than two days after snowmelt.

Site 1, the salt marsh, was covered by surface water for most of the active period, and water content of samples was not recorded. The nitrogen fixation activity correlated well with air temperature (Table 2) as long as water content was not limiting. Nitrogen fixation reached a peak on 26 June, corresponding with the first relatively warm period, and a higher peak around 13 July, which represents the next warm period. The following week, the site went rapidly from saturated with water to very dry and activity reached zero due to lack of water between 19 and 25 July (Fig. 3A).

The vegetation at Site 2 was covered by melt water for two weeks from about 11 June to 25 June. It was possible to take samples under the water on 17 June. At this time the samples already had some nitrogen fixation activity that increased with increasing temperature, but then decreased as water content declined (Fig. 3B). We could only see significant correlation between activity and temperature before water started to become limiting (Table 2). Nitrogen fixation activity and water conditions were correlated for the period of decreasing water content (Table 2), and nitrogen fixation was close to zero when the water content of the samples went below 60%.

Site 3, the dry meadow, had lower activity than Site 2, but the time course for activity and water content follow the same patterns as for Site 2 (Fig. 3C); again activity correlated significantly with water content in the desiccation period (Table 2). In the period when water conditions were not limiting, nitrogen activity correlated with temperature (Table 2).

Nitrogen fixation activities at Site 4 were not limited by water, and stayed above 80% water content through the whole period. Furthermore, nitrogen fixation activity correlated with the air

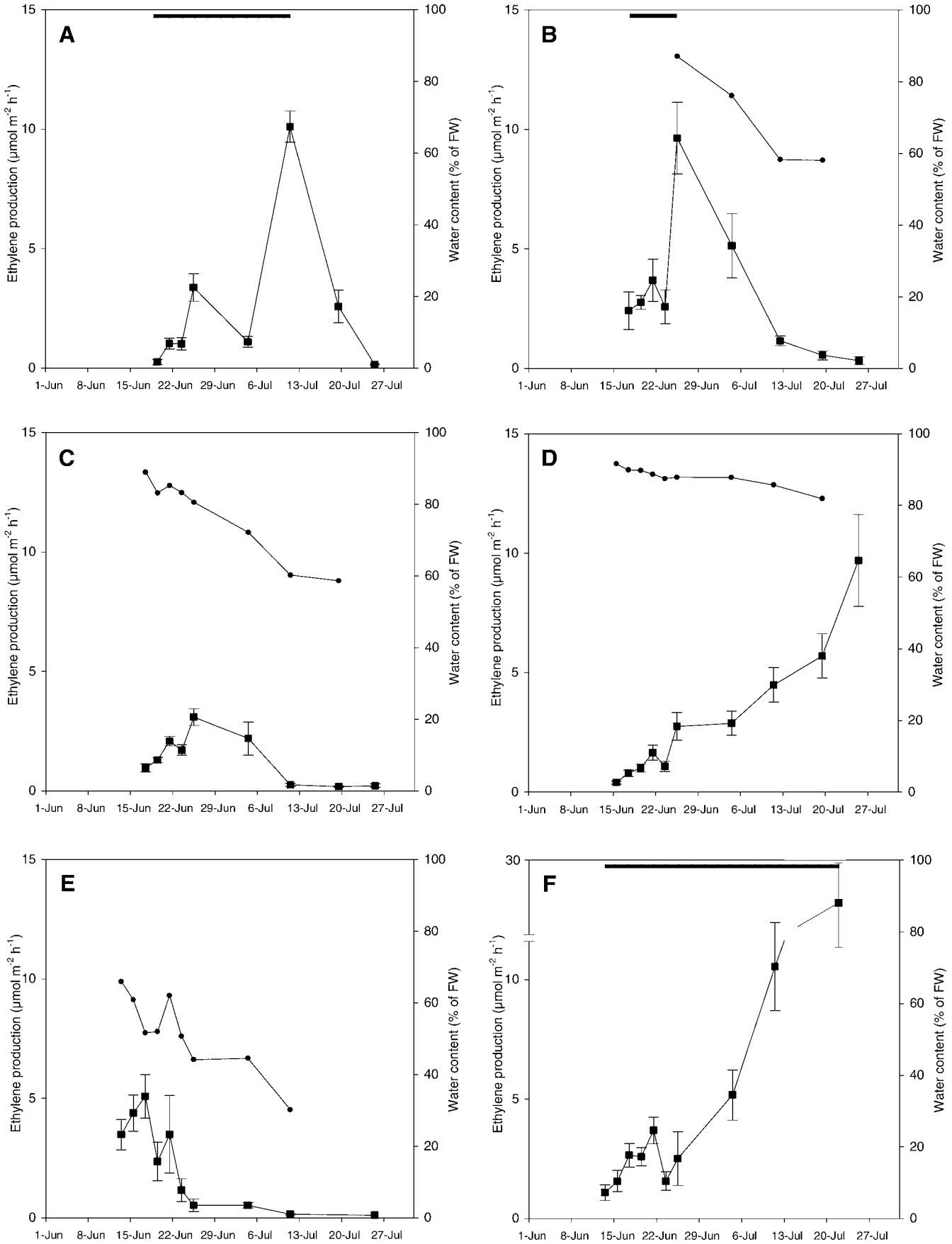

FIGURE 3. Ethylene production (■) and water content (●) of the vegetation at the sites. Site 1 (A), Site 2 (B), Site 3 (C), Site 4 (D), Site 5 (E), and Site 6 (F). Horizontal bars indicate periods with surface water where water content was not measured. Values for ethylene production are means (n = 5) ± SEM (Standard Error of the Mean). Note well: The scale of Y-axis in Figure F has been changed for better clarity.

temperature with a time-lag of one day through the whole period (Fig. 3D, Table 2).

The cryptobiotic crust at Site 5 was the most extreme site with respect to water content. Immediately after snowmelt Site 5 had relatively high water content and nitrogen fixation activity, followed by fast desiccation and decrease of nitrogen fixation activity (Fig. 3E). Activity was correlated with water during the desiccation period (Table 2). Furthermore, the nitrogen fixation activity was clearly above zero until water content of the samples went below 50%. The desiccation of this site happened so fast that we could only obtain three observations during the wet period, but there was a good correlation between activity and temperature for this short period (Table 2).

The highest nitrogen fixations activity was found at Site 6, the flushed meadow, which contained both free-living and epiphytic cyanobacteria. Nitrogen fixation activity through the whole period correlated with the air temperature with a time-lag of one day (Fig. 3F, Table 2). Water content of samples was not measured since the site was flushed with water through the entire season (Fig. 3F).

Estimation of the total amount of ethylene produced during the first 40 days after the snowmelt varied significantly among most of the sites (Fig. 4). The highest production of ethylene was found at Site 6, the wettest site and the only one with surface water during the entire study period. Sites 1 and 2, which initially were saturated with water, and Site 4 that stayed moist the whole period, had less than 43% of the ethylene production of Site 6 (Fig. 4). Sites 3 and 5 were the driest sites and had also the lowest total ethylene production during the period (Fig. 4). Based on One-way ANOVA and post hoc tests of the total ethylene production, the sites could be divided into three activity groups (Fig. 4).

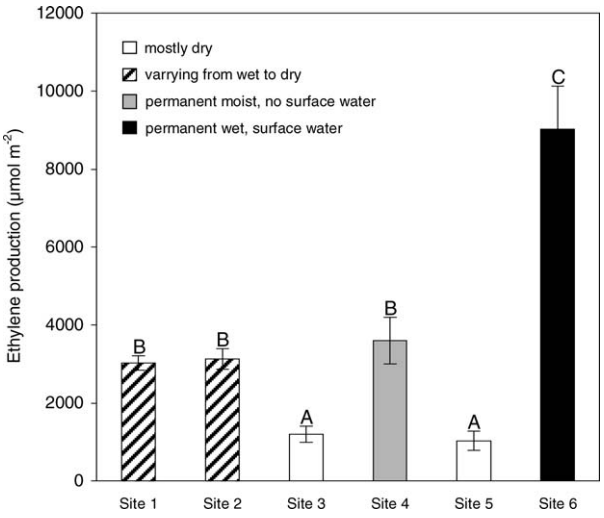

FIGURE 4. Estimated total ethylene production at different sites for the first 40 days after snowmelt. Values for ethylene production are means (n = 5) ± SEM. Same letters (A, B, C) indicate sites without significant differences in ethylene production (n = 5, DF = 5, F = 28.41, $p \leq 0.05$).

Discussion

In a previous study, Zielke et al. (2002) described the influence of abiotic factors on biological nitrogen fixation in samples from the same field sites as the present study. They found that vegetation samples from all sites showed potential for nitrogen fixation under laboratory conditions. However, this potential might not reflect the actual amount of nitrogen fixed under different environmental conditions in the field. In the present study, we revealed that site-specific variations in nitrogen fixation activity might be ascribed to different factors, which can be divided into three interconnected categories. These are based on water status of the vegetation, type of vegetation, and the size and structure of the cyanobacterial community.

The seasonal onset of nitrogen fixation at the different sites in the spring depended on snow conditions, and consequently, on the start of the snowmelt. The snow melted first at the highest site and last at the lowest site in the transect. As soon as the temperature in the vegetation was above zero, the cyanobacteria became active and started to fix nitrogen. During the early phase after snowmelt, when water was not a limiting factor, nitrogen fixation activity increased with time at all sites and, in most cases, nitrogen fixation activity correlated with temperature in this phase. The length of this period was determined by the water status of the vegetation and the type of vegetation. At Sites 2, 3, and 5, the phase of no-water limitation was followed by a rapid desiccation associated with a decrease in nitrogen fixation activity. At Site 5, the cryptogamic crust, the wet phase was extremely short, meaning that nitrogen fixation activity was detectable for less than two weeks, even though this type of vegetation had activity at lower water content than at Sites 2 and 3. In all sites with desiccation periods, the nitrogen fixation activity was correlated with water content, and in these types of vegetation, activity is strictly regulated by available water (Table 2). In contrast, Sites 1, 4, and 6 had a high water status for a longer period and nitrogen fixation became controlled by air temperature (Table 2). In the case of Sites 4 and 6, the correlation between these two factors showed a time-lag of one day; this may be due to a lag in the heating of the water-saturated vegetation. In contrast, no delayed effect of changes in air temperature at Site 1 could be found. This is probably due to the fact that this site was dominated by free-living cyanobacteria forming small beads on a dark silt layer, which may transfer the heat more rapidly to the organisms. Finally, Site 1 dried out within a short period, which consequently led to a rapid decline in nitrogen fixation activity. During the wet period while no sites were limited by water, the nitrogen fixation activity on any given day varied between sites.

Based on the overall nitrogen fixation activity, represented by the total amount of ethylene produced during the study period, the six sites can be divided into three groups (Fig. 4). The first group (A), including Sites 3 and 5, represents the driest sites, and is also characterized by the lowest total amount of produced ethylene. The next group (B), consisting of sites with variable water status from wet to dry but without surface water throughout the entire season (Sites 1, 2, and 4), showed about a threefold overall nitrogen fixation activity as the dry sites. The final group (C) contains only Site 6, which is characterized by flowing surface water throughout the study period. This permanent water saturation is associated with the highest production of ethylene.

A coarse vegetation map covering the study sites allows a simple up-scaling of our results. Salt marshes (Site 1) are limited to beach areas close to the sea and comprise a small part of the total vegetation in the open valleys of the west coast of Spitsbergen. Utilizing Landsat-5 TM data (Jacobsen and Elven, personal communication; Linn Bryhn Jacobsen, Norwegian Pollution Control Authority (SFT), Box 8100 Dep, 0032 Oslo, Norway) found the distribution of xeric, mesic, and hydric-hygric vegetation on the west coast of Spitsbergen to be 22, 40, and 33%, respectively. Site 5, the cryptogamic crust, is definitely a xeric type of vegetation, while Sites 2 and 4 are mesic. Site 3 is in between xeric and mesic, and Site 7 is hydric-hygric. Even a very coarse classification of the water status of the vegetation gives an idea of the extent of areas where the nitrogen fixation may be limited by the amount of water in the vegetation.

However, the total amount of fixed nitrogen and the course of nitrogen fixation activity do not solely depend on the environmental conditions, i.e., the water regime and the air temperature, but also on the cyanobacterial community and its adaptation to environmental factors. Although the nitrogen fixation activity at Sites 2, 3, and 5 responded instantaneously to changes of the water conditions in the vegetation

(Figs. 3B, C, and E), two different response patterns could be found. While at the moss-dominated Sites 2 and 3, nitrogen fixation activity stopped at a water content of about 60% (Figs. 3B and C), but nitrogen fixation activity continued at Site 5 even when the water content reached values below 50% (Fig. 3E). This may be due to a better adaptation of the components of the cryptobiotic crust to low water status, as previously described for several species of cyanobacteria and mosses (Brock, 1975; Potts, 1994; Robinson et al., 2000, 2003). Site 1 had mainly free-living cyanobacteria, while Sites 2, 3, and 4 had mainly cyanobacteria associated with mosses. The high activity at Sites 1 and 2 may have been caused by heat storage of the meltwater standing above the vegetation. The time-delay at Site 1 was due to later snowmelt. The standing water resulted in a stable temperature of around 10°C in the water, while the air temperature was between 2 and 6°C. Site 3 followed the same pattern as Site 2, but with much lower activities. This site had no free water covering the site after snowmelt, and the temperature of the vegetation layer was more directly influenced by the air temperature and the underlying permafrost. Site 5, the cryptobiotic crust, dried out very quickly after snowmelt. Since it is not possible to estimate the activity that the sites could have attained if water had not limited activity, it is only the final activity at Sites 4 and 6 that can be directly compared. Site 6, with a combination of free-living and moss-associated cyanobacteria, reached more than twice the activity (28 μmol m^{-2} h^{-2}) than at Site 4 (10 μmol m^{-2} h^{-2}) with only moss-associated cyanobacteria.

Conclusions

The course and the temporal variations of nitrogen fixation activity at the different sites may be influenced by several environmental and biological factors. In the period just after snowmelt the vegetation is saturated with water, and this period is the most important in respect to nitrogen fixation for much of the vegetation. In areas that remain wet through the entire growing season, nitrogen fixation is controlled by air temperature.

The light and temperature conditions are nearly the same at all sites, and our results confirm that under field conditions the nitrogen fixation activity is strongly affected by the availability of water. However, different types of vegetation harbor different cyanobacterial communities, which may vary in their adaptation to water availability.

Considering the low precipitation on Svalbard during summer, most habitats experience long periods of desiccation. Detailed vegetation maps based on remote sensing together with extended measurements of nitrogen fixation in different types of vegetation throughout the growing season will enable estimations of nitrogen fixation on a landscape scale.

Factors affecting the water status of arctic soils and vegetation, such as start of the snowmelt, topography, and the amount and duration of precipitation, have to be taken into account when predicting the effect of the climate change on terrestrial nitrogen fixation in the Arctic.

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