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# N/P Addition Is More Likely than N Addition Alone to Promote a Transition from Moss-Dominated to Graminoid-Dominated Tundra in the High-Arctic

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**Abstract:** Nutrient availability for tundra vegetation could change drastically due to increasing temperatures and frequency of nitrogen deposition in the Arctic. Few studies have simultaneously examined the response of plant communities to these two pressures over a long period. This study aims to assess which driver between increasing nitrogen (N) and phosphorus (P) availability through global warming and increasing N availability alone via N deposition is more likely to transform arctic wetland vegetation and whether there is a time lag in this response. An annual fertilization experiment simulating these nutrient inputs was conducted for 17 years in the Canadian High-Arctic to assess the impact on aboveground net primary productivity, floristic composition, and plant nutrient concentration. While the primary productivity of mosses remains unchanged by fertilization after 17 years, productivity of graminoids was increased slightly by N addition (36% increase at the highest dose). In contrast, the primary productivity of graminoids increased strongly with N/P addition (over 227% increase). We noted no difference in graminoid productivity between the 2nd and 5th year of the experiment, but we observed a 203% increase between the 5th and 17th year in the N/P addition treatments. We also noted a 49% decrease in the total moss cover and an 155% increase in the total graminoid cover between the 2nd and 17th year of N/P addition. These results indicate that the impact of warming through increased N/P availability was greater than those of N deposition alone (N addition) and promoted the transition from a moss-dominated tundra to a graminoid-dominated tundra. However, this transition was subject to a time lag of up to 17 years, suggesting that increased productivity of graminoids resulted from a release of nutrients via the decomposition of lower parts of the moss mat.

**Keywords:** nitrogen deposition; global warming; nutrient availability; fertilization; arctic tundra; productivity; time lag; transition; disturbance; community

## 1. Introduction

The Arctic is an extreme environment for vegetation. Low temperatures, minimal shelter, a low incidence angle of sunlight, and the presence of permafrost are factors that,

in combination, restrict vegetation growth [1]. The low availability of nutrients to plants is another critical component influencing the primary productivity of the tundra [1]. This limitation results from physical and chemical properties of Arctic soils. Most Arctic soils are characterized by acidic conditions, poor drainage, and high organic matter content [2]. Moreover, decomposition and mineralization processes are restrained due to low temperature [3,4] and poor drainage conditions [5], which limit microbial activity [6,7]. For example, in Toolik Lake, Alaska, nitrogen (N) and phosphorus (P) pools range from 22 to 133 g N m$^{-2}$ and from 2 to 15 g P m$^{-2}$ in tundra soils [8]. In temperate and boreal soils of eastern Canada, N pools range from 475 to 1261 g N m$^{-2}$ [9], and in boreal soils, P pools range from 9 to 12 g P m$^{-2}$ [10]. Therefore, growing evidence is showing that N and P are both co-limiting to vegetation and microbial life in the tundra biome [11,12].

Nutrient limitation of the tundra could be modified by climate change. The Arctic is warming at a rate more than twice as fast as the global average [13]. While higher temperatures can directly promote plant productivity in the tundra by providing a warmer environment for vegetation [14], warming can indirectly enhance plant productivity by stimulating microbial decomposition of organic matter and releasing more nutrients for vegetation uptake and growth [14–16]. Warming leads to a deepening of the active layer of the soil [17–19] and more rapid mineralization of nutrients, leading to the fertilization of an ecosystem traditionally limited by the availability of N and P [20–22] rather than by other elementary nutrients and micronutrients [23]. Moreover, a study in the Alaskan tundra showed that warming using greenhouses and N/P fertilization had similar effects, as both promoted the biomass and growth of vascular plants equally [24].

In addition to the indirect effects of global warming on nutrient availability, the increase in anthropogenic activities such as maritime transport in the Canadian Archipelago [25] and exploitation of natural resources [26,27], and precipitations [28] appear to increase the frequency and intensity of N deposition events on the tundra [29]. Since much of this deposition occurs during the summer, when vegetation sequesters most of the N, this could exacerbate the effects of this N enrichment. Therefore, even relatively modest increases in current (0.1 to ~1 g m$^{-2}$ year$^{-1}$) [29] and future N inputs can represent a significant addition to this nutrient-poor environment [30].

The consequences of an increase in nutrients availability via the fertilizing effect of N deposition (N addition) and global warming (N/P increase through mineralization) are numerous. An increase in nutrient availability promotes vascular plant productivity, increases aboveground biomass, and could act as a net carbon source under certain conditions [17–19]. Other functional groups, however, such as mosses and lichens, tend to decrease in abundance and cover in response to N deposition [31–33] and in response to global warming [34–38]. This negative impact on mosses and lichens could be explained by the increasing nutrient availability, which causes enhanced plant productivity and, in the longer term, to the competitive exclusion by taller growing species [39]. In general, vascular species such as grasses (*Poaceae*) and sedges (*Cyperaceae*) are largely promoted, while bryophytes and lichens are disadvantaged [39].

Many studies simulating the indirect effects of global warming on nutrient availability do not accurately reproduce the magnitude of future temperature increases, as nutrients have generally been added in amounts (e.g., >10 g N m$^{-2}$) greater than the anticipated increase under global warming projections [40]. As an indicator, in wet/acid tundra, an increase in mean temperature of 3 °C would be equivalent to an addition of 7 g N m$^{-2}$ annually [18]. Moreover, most of these studies were short term (i.e., less than five years) [40], and short-term responses to nutrients manipulations do not reliably mimic long-term responses [41]. Finally, few studies have examined the temporal change of plant communities following different fertilization treatments over a decade.

The first objective of this study was to determine, over almost two decades (17 years), whether an increase in N/P availability due to the indirect effect of global warming or an increase in N-only availability due to the direct effect of N deposition was likely to be the most influential driver of changes in wetland plant communities in the Canadian

High-Arctic. To do so, we evaluated the effect of N addition and N/P addition treatments on aboveground net primary productivity (ANPP), floristic composition, species cover, and plant chemistry after 17 years of fertilization. We hypothesized that N/P addition should lead to greater changes in tundra wetland vegetation than N addition alone in a system such as the Arctic, which is known to be highly co-limited in N and P availability [11,12]. The second objective was to assess if there was a lag in the response time of plant communities to these two drivers by examining the changes on ANPP and plant chemistry concentration after 2, 5, and 17 years of fertilization. We hypothesized that the change on vascular plants was not immediate because mosses should sequester most of the nutrients initially [42,43] but the decomposition of the lower parts of the mosses mat should eventually allow graminoids to access those nutrients.

## 2. Materials and Methods

### 2.1. Study Area

The study took place on Bylot Island (73°08′ N, 80°00′ W), part of the Sirmilik National Park in Nunavut, in the Canadian Arctic Archipelago, a productive High-Arctic ecosystem [44]. The study area is characterized by a mosaic of freshwater wetlands composed of peat polygons, small lakes, and pond aggregations surrounded by upland, mesic vegetation [45,46]. The microtopography that develops within these landforms has a significant influence on the movement of surface water. Consequently, this affects the hydrological and thermal soil conditions, which impact plant communities [47,48]. These wetlands are fed by snowmelt runoff from the surrounding hills and are characterized by arctic fens vegetation [43]. They are dominated by *Cyperaceae* (*Carex aquatilis* Wahl., *Eriophorum scheuchzeri* Hoppe), *Poaceae* (*Dupontia fischeri* R. Br., *Arctagrostis latifolia* R. Br., Griseb., *Pleuropogon sabinei* R. Br.), and brown mosses (*Aulacomnium acuminatum* (Lindb. et Arnell) Kindb., *Aulacomnium turgidum* (Wahl.) Schwägr., *Scorpidium revolvens* (Sw) Rubers., *Scorpidium cossonii* (Schimp.) Hedenäs., *Campylium stellatum* (Hedw.) C.E.O. Jensen., *Polytrichum swartzii* Hartm.) [43,49].

The average summer temperature at the study site is 4.5 °C and −32.8 °C in winter [50,51]. In addition, between 1976 and 2011, the temperature of the region warmed by an average of 2.8 °C in spring/summer and 4.3 °C in autumn [50]. Snow cover is present from October to early June. From 1995 to 2019, the average amount of rain between 1 June and 17 August was 77.5 mm. There is no annual trend in the region, and the total summer precipitation actually decreased by 21 mm per decade on the island from 1995 to 2019 [52]. In contrast, Arctic precipitation rates are predicted to increase over the next decades [28]. The Greater Snow Goose is the principal herbivore in the tundra wetlands of the island [50].

### 2.2. Experimental Design and Fertilization

A randomized complete block experimental design was set up in 2003 in the Qarlikturvik Glacial Valley and was maintained for 17 years (Figure 1). Six blocks were randomly positioned in different polygon fens at least 500 m apart from each other. Each block comprised six main plots of 4 $m^2$, randomly arranged and separated by at least 5 m. Each plot was protected from grazing and grubbing by geese with a chicken-wire fence (2.5 cm mesh size, 1 m high) since the beginning of the experiment in 2003 to isolate the fertilization effect from any grazing effect, and to avoid nutrient addition through feces. Each plot of a block received a different annual fertilization treatment for 17 years, which were replicated in all blocks. The fertilizer treatments presented in Table 1 were applied at the beginning of each growing season (late June or early July) between 2003 and 2019 after standing water resulting from spring runoff had disappeared from the plots.
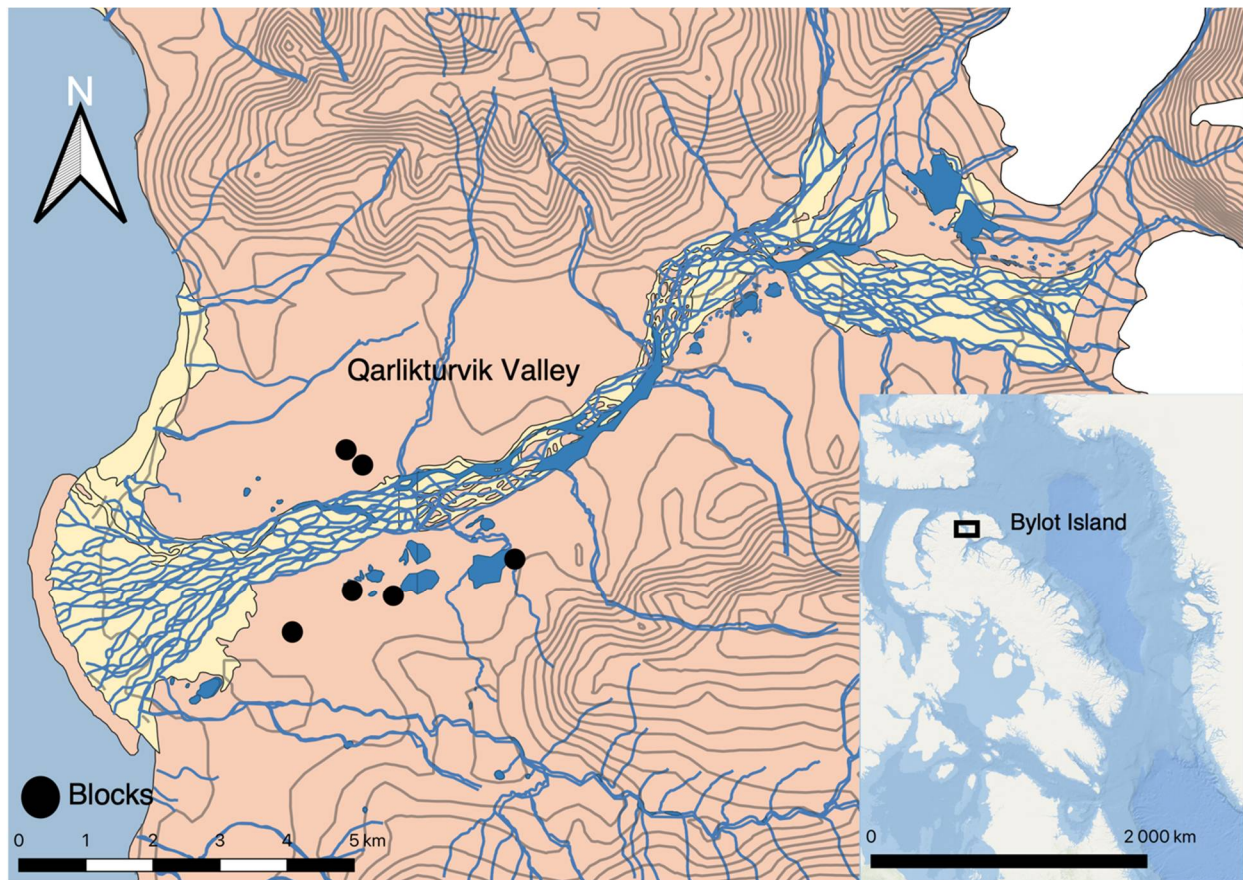
**Figure 1.** Location of the six experimental blocks located in the wetlands of the Qarlikturvik glacial valley, on Bylot Island (Nunavut, Canada).

**Table 1.** List of fertilization treatments, the context associated with each treatment, and the amount of N and P in m$^2$ applied annually in each experimental block for 17 years in the tundra wetlands of Bylot Island, Nunavut.

| Fertilization Context | Nutrient Addition Treatment | N (g m$^{-2}$ Year$^{-1}$) | P (g m$^{-2}$ Year$^{-1}$) |
|---|---|---|---|
| Control | CT | 0 | 0 |
| N addition | N1 | 1 | 0 |
| | N3 | 3 | 0 |
| | N5 | 5 | 0 |
| N/P addition | NP3 | 3 | 0.5 |
| | NP5 | 5 | 1 |

Inorganic N was applied as ammonium nitrate (34-0-0) ($NH_4NO_3$) and inorganic P as superphosphate (0-46-0) ($H_3PO_4$). The inorganic N was diluted in 2 L of water before application with a garden watering can. For hydrological consistency, control plots also received 2 L of water. The inorganic P was applied manually and uniformly over the entire experimental plot. The N1, N3, and N5 treatments were designed to test the direct fertilizing effect of N deposition via N addition alone on vegetation and its variability. In comparison, current N deposition rate in the Arctic is around 0.1 to ~1 g N m$^{-2}$ year$^{-1}$ [29] and is around 0.75 to ~4 g N m$^{-2}$ year$^{-1}$ in the alpine tundra of Europe [53]. Therefore, although the N level used here may seem high, it could reflect extreme levels to be encountered locally in the future in the context of increasing N deposition worldwide [54]. N level was also selected based on levels found to affect plant growth in the Arctic in previous

fertilization experiments [55–60]. The NP3 and NP5 treatments were designed to test the indirect fertilizing effect of global warming through N/P addition on vegetation, assuming they mimicked the greater soil mineralization of N and P expected under a warming environment. In comparison, as mentioned before, in wet/acid tundra, an increase in mean temperature of 3 °C would be equivalent to an addition of 7 g N m$^{-2}$ [18,61]. In addition, in boreal *Sphagnum*-dominated peatlands (another nutrient poor ecosystem), the effect of an annual N enrichment of about 4 g N m$^{-2}$ y$^{-1}$ on *Sphagnum* productivity was equivalent to the one of a temperature increase of 1 °C [62]. Although P cycling is probably less sensitive to temperature increases [16] than N, summer warming has been shown to stimulate P release from litter [63] and P mineralization as phosphatase enzyme activities in soil increased with temperature [64]. For example, in Tuktoyaktuk (69° N), it has been estimated that between 0.41 and 1.49 g P m$^{-2}$ is released annually into the soil [65]. Furthermore, in the boreal forest, an increase in temperature of 1 °C increased P availability by 7% [64]. Thus, a rise of 3 °C could release between 0.5 à 1.8 g m$^{-2}$ year$^{-1}$ of P. Considering that by 2100, Arctic surface air temperature should have increased by more than 3 °C [66], the amount of N and P released by warming of the active layer is likely to be similar in magnitude to our fertilizer treatments.

### 2.3. Aboveground Net Primary Productivity (ANPP)

We harvested the biomass from each plot at peak production (1–15 August 2019), as this is a good estimate of ANPP for vascular plants in the High-Arctic [67]. Within each experimental block, we collected the biomass samples of all treatments on the same day. Thus, the differences in sampling date were between blocks and not within blocks. For vascular plants, we randomly collected two 100 cm$^2$ square samples in each plot to a depth of 10 cm. The graminoid biomass, which accounted for >90% of total vascular plant biomass in those fens [67], was sorted by graminoid family (*Cyperaceae* and *Poaceae*). We retained only the aboveground biomass, which includes the green leaves and the green and white parts of the stems above the last growth meristem. We dried the sorted biomass samples in paper envelopes for 24 h at 50 °C or until a constant weight was reached, and then weighed them to estimate the ANPP of graminoid plants (g m$^{-2}$ year$^{-1}$).

To estimate the ANPP of mosses, we collected three 15 cm$^2$ cores (*area*), 9 cm deep, in each plot at the same time graminoid plants were sampled. On each core, we measured the height (*height*) of the photosynthetic part, corresponding to the green part of the mosses, with a ruler (+/− 1 mm) at ten points around the core to obtain the average height of the living mosses. We then cut and dried the photosynthetic part in paper envelopes for 24 h at 50 °C or until a constant weight was reached to obtain the dry biomass (*biomass*). We used two different methods to measure the average annual moss elongation. First, we measured moss elongation (*elongation*) using natural markers of growth present in some moss species (*Polytrichum swartzii* and *Meesia triquetra* (L. ex Jolycl.) Ångström), which show clear patterns of annual growth [68]. When at least three homogeneous clusters of these two species were present, we collected ten stems per cluster of *P. swartzii* or *M. triquetra* in each plot simultaneously at the core sampling location. We measured the moss elongation between natural markers with an electronic caliper (+/− 0.01 mm) on the fresh specimen under the binocular. When *P. swartzii* or *M. triquetra* homogeneous clusters were absent or in insufficient quantity (<three clusters), we measured moss elongation using cranked wires (bent stems) as artificial markers [69]. In the plots where species with natural markers were in insufficient quantity (40% of plots), we installed and measured up to three clusters of seven cranked wires at the beginning of the growing season, and we measured them again at the end of the growing season to estimate the moss mat elongation. Natural markers provide a better estimate of moss growth than the cranked wires under Arctic conditions [68]. Artificial markers are subject to errors due to permafrost heaves, animal disturbance, and observer effects, but the chicken-wire fence protected the plots

from animal disturbance and the same observer took all the elongation measurements. We estimated the moss ANPP ($g\,m^{-2}\,year^{-1}$) according to the following equation:

$$moss\ ANPP = (biomass \times elongation)/(area \times height), \qquad (1)$$

### 2.4. Vegetation Composition

We randomly positioned two $625\ cm^2$ square quadrats in portions of each plot that had never been sampled before. We estimated the cover percentage of each species of vascular plants (up to 100%) and mosses (up to 100%) to the nearest 1%, although we merged some taxonomic groups such as lichens and willows for analyses. A list of all the species encountered is available in Table A1.

### 2.5. Chemical Analyses

We measured the N and P concentration in the aerial parts (leaves and stems) of *Cyperaceae* and *Poaceae* and in the green part of mosses after 17 years of fertilization. Dried biomass samples (see above) were brought to the Plant Science Department of Université Laval and were used to measure N and P concentration after 17 years of fertilization. Samples were ground and N concentration analyzed by applying first a micro-kjeldahl digestion with a *Tecator 2020 Digestor* and then by colorimetry using the Microplate Spectrophotometer *Biotek Epoch 2* [70,71]. We determined the P concentration by digestion in nitric and perchloric acids followed by a colorimetry assay with the same microplate spectrophotometer [72].

### 2.6. Statistical Analysis

We used a series of linear mixed models for random complete blocks to explore the main effect of fertilization, graminoid family (*Cyperaceae* and *Poaceae*) and their interactive effects [73] on graminoid and moss ANPP, and nutrient concentration. Simple and linear a priori contrasts were performed to compare the effects of N addition alone (N1, N3 and N5 combined, and the linear response of increasing N addition) and N/P addition (NP3 and NP5 combined) on the different variables. We characterized vegetation communities using a principal component analysis (PCA) with the proportions of species measured by the vegetation censuses. We associated a posteriori certain species groupings defined by the PCA with the fertilization context (N addition or N/P addition). We performed a Hellinger transformation on the species abundance data prior to the PCA to account for double absence [74].

We also wished to study the temporal change of plant communities in response to increased nutrient availability. To do so, we compared the response variables obtained after 17 years of fertilization (present study) with data collected in the same treatment plots after 2 years of fertilization [43] and 5 years of fertilization [49]. The technique used here was the resampling method, also called "snapshot resampling" [75]. This assumes that the noise associated with inter-annual variability in the response variables was small relative to the signal induced by long-term change. Snapshot resampling can sometimes yield spurious conclusions [75]. However, the accuracy of results increases when inter-annual variability in the response variable is low or if the magnitude of change through time is high [75], as we expected with our fertilization treatments. Therefore, we explored the effects of time (categorical variable: 2, 5, and 17 years), fertilization, and their interactions on graminoid and moss ANPP and nutrient concentration with linear mixed models. We examined vegetation cover changes between the 2nd and 17th year of fertilization for each species and treatment using paired-sample t tests on proportion. We also compared total moss and graminoid cover change in proportion between the 2nd and 5th year, the 5th and 17th year, and the 2nd and 17th year of fertilization for each treatment using paired-sample t tests on proportions. We used a sequential Bonferroni correction (Holm-Bonferroni Method) for multiple comparisons to adjust the significance level depending on the number of comparisons made [76]. All analyses were performed in R v.3.2.6 [77]

using the software packages *ggplot2* [78], *lme4* [79], *vegan* [80] and *FactoMineR* [81]. For all analyses, we considered *p* values < 0.05 as statistically significant except when a sequential Bonferroni correction was applied. Finally, we tested the assumptions of normalized residuals, leverage, and Cook distances for all models.

## 3. Results

### *3.1. Aboveground Net Primary Productivity (ANPP)*

#### 3.1.1. Fertilization Effect after 17 Years

There was an interaction between the effects of fertilization treatments and graminoid family on ANNP of graminoids after 17 years (Table 2). ANPP of *Cyperaceae* increased by 100% on average in the N addition treatments (mean of N1, N3 and N5) but not *Poaceae*, whereas the ANPP of *Poaceae* increased by 277% on average in the N/P addition treatments (mean of NP3 and NP5) but not *Cyperaceae* (Figure 2). After 17 years, the ANPP of *Cyperaceae* increased by 40% in the N1 treatment compared to the control, whereas the ANPP of *Poaceae* decreased by 26% (Figure 2). N addition linearly promoted the ANPP of graminoids, leading to a 36% increase over the control in the N5 treatment after 17 years of fertilization (Table 2; Figure 2). The increase in graminoid ANPP was also much greater in the N/P addition treatments than in the N addition treatments (Table 2). ANPP of mosses in the N/P addition treatments was 83% higher than in the control, but no effect of N addition alone on ANPP of mosses was noted after 17 years of fertilization (Table 2; Figure 2). However, the ANPP of mosses in the N1 treatment tended to increase by 44% compared to the control after 17 years of experimentation (Figure 2).

**Table 2.** Results of linear mixed models evaluating the effects of (A) fertilization after 17 years, graminoid family (*Cyperaceae*, *Poaceae*) and their interaction, and (B) fertilization, time after initiation of the experiment (2, 5 and 17 years) and their interaction on the aboveground net primary productivity (ANPP) of graminoid plants and mosses in the tundra wetlands of Bylot Island, Nunavut. (C) A priori contrasts were also applied on fertilization effects after 17 years.

| | Graminoid | | | Moss | | |
|---|---|---|---|---|---|---|
| | **ANPP** | | | **ANPP** | | |
| | *F* | *P* | **df** | *F* | *P* | **df** |
| A. Fertilization effect after 17 years | | | | | | |
| Fertilization (F) | 3.9 | 0.0046 | 5, 54 | 0.8 | 0.0901 | 5, 25 |
| Family (Fa) | 4.8 | 0.0314 | 1, 54 | | | |
| F × Fa | 3.7 | 0.0062 | 5, 54 | | | |
| B. Temporal effect of fertilization | | | | | | |
| Fertilization (F) | 9.5 | <0.0001 | 5, 85 | 1.0 | 0.4075 | 5, 85 |
| Time (T) | 9.7 | 0.0002 | 2, 85 | 26.0 | <0.0001 | 2, 85 |
| F × T | 2.1 | 0.0356 | 10, 85 | 0.8 | 0.6008 | 10, 85 |
| C. Contrasts | *t* | *P* | **df** | *t* | *P* | **df** |
| Nitrogen linear | 2.4 | 0.0318 | 15 | 0.1 | 0.9874 | 15 |
| Control vs. N addition [1] | 0.5 | 0.6224 | 54 | 0.9 | 0.3630 | 25 |
| Control vs. N/P addition [2] | 2.5 | 0.0171 | 54 | 2.7 | 0.0136 | 25 |
| N addition vs. N/P addition | 2.7 | 0.0102 | 54 | 2.4 | 0.0246 | 25 |

[1] N1, N3, and N5 are grouped under the term "N addition". [2] NP3 and NP5 are grouped under the term "N/P addition".

#### 3.1.2. Temporal Effect of Fertilization

There was a significant interaction between the effects of fertilization treatments and time on the ANPP of graminoids (Table 2). Although there was no difference in the ANPP of graminoids following 2, 5, or 17 years in the N addition treatments, the ANPP of graminoids in the N/P addition treatments was on average 177% higher after 17 years than after 5 years of fertilization, whereas no difference was observed between the 2nd and the 5th year (Figure 3). However, ANPP of graminoids in the control also increased by 75% between

5 and 17 years of fertilization (Figure 3). ANPP of mosses after 5 years of fertilization was 188% higher than after 2 years and 27% higher than after 17 years, but there was no interaction between fertilization treatments and time (Table 2, Figure 3).
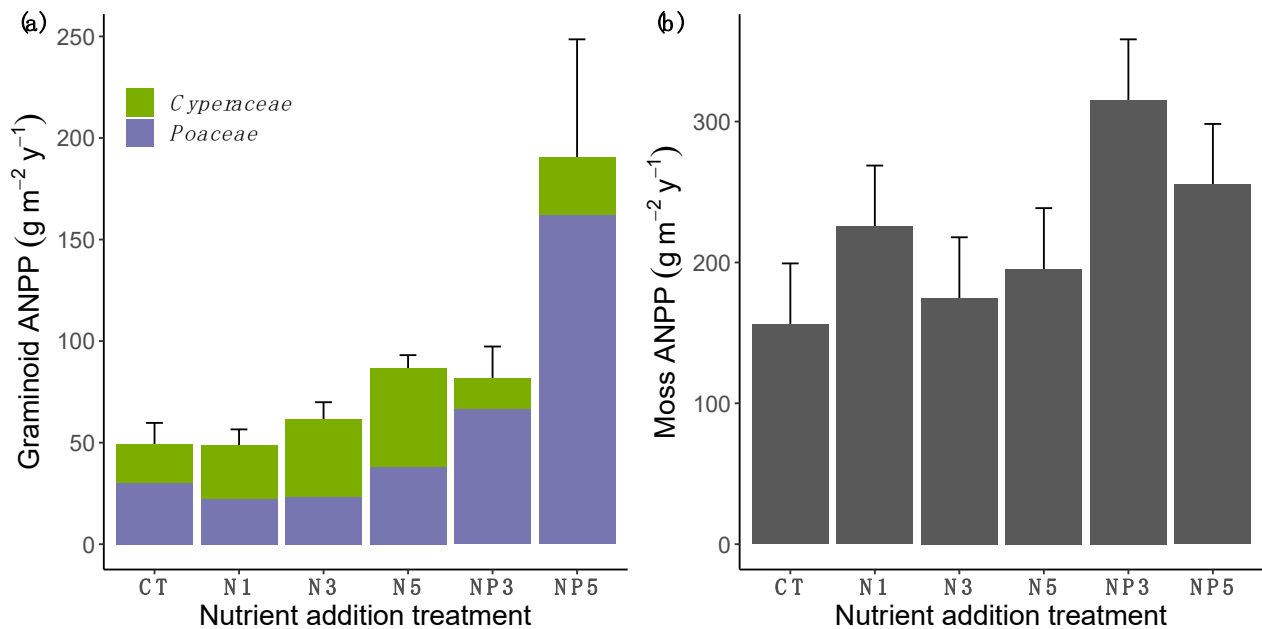


**Figure 2.** Aboveground net primary productivity (ANPP) of (**a**) graminoids separated by graminoid family and (**b**) mosses according to fertilization treatments after 17 years of experimentation in the tundra wetlands of Bylot Island, Nunavut. Least square means + SE are presented. See Methods for definition of treatments.
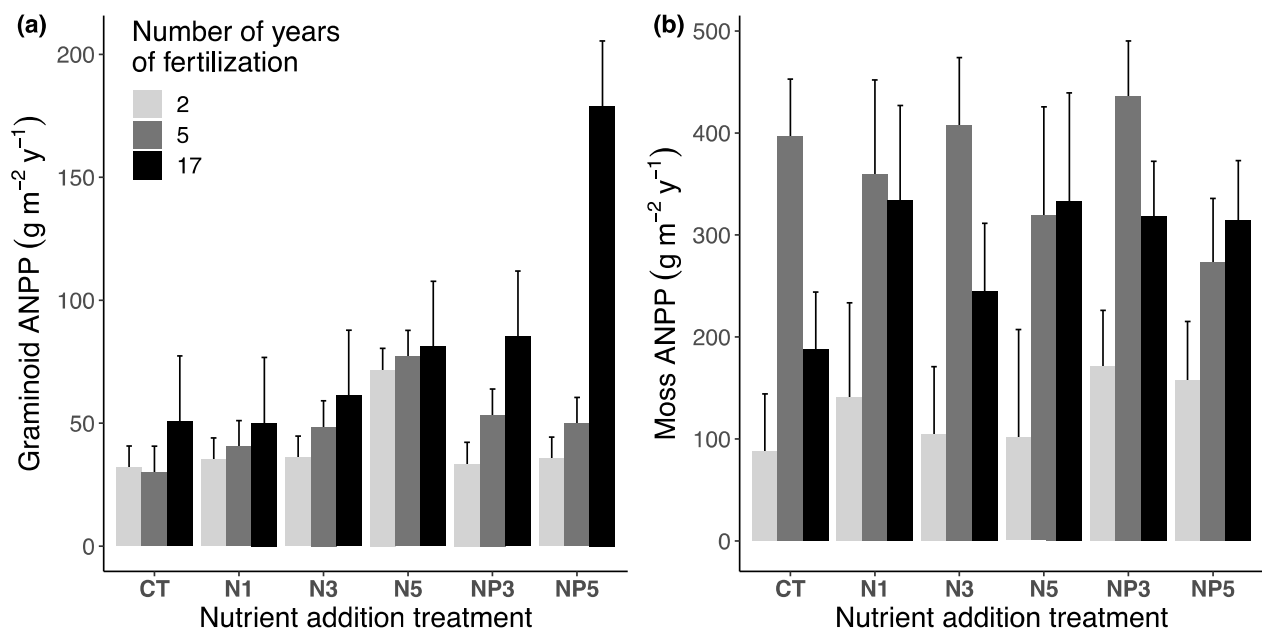


**Figure 3.** Aboveground net primary productivity (ANPP) of (**a**) graminoids and (**b**) mosses after 2, 5, and 17 years of experimentation according to fertilization treatments in the tundra wetlands of Bylot Island, Nunavut. Least square means + SE are presented. See Methods for definition of treatments.

*3.2. Vegetation Composition*

The first two axes of the PCA analysis explained 37% of the proportion of variance in species composition in our plots (Figure 4). Axis 1 (PC1) was negatively associated

with *A. acuminatum* and positively associated with *S. revolvens*, *S. cossonii* and to a lesser extent *Calliergon giganteum* (Schimp.) Kindb. and *C. aquatilis*. Axis 1 was mainly associated with brown moss species that preferentially develop under different hydric and mineral conditions such as the genus *Scorpidium* (positive values), found more in wet and poor fens and the genus *Aulacomnium* (negative values) found more in dry and rich fens [82]. Axis 2 (PC2) was negatively associated with *Poa arctica* R. Br. and was positively associated with *E. scheuchzeri*, and *D. fisheri* (Figure 4, Table A3). According to the PCA, there were some differences in vegetation composition between the different fertilization contexts (Figure 4). Mainly, the vegetation in the N/P addition plots (NP3 and NP5) was distinct from the control along Axis 1 but not the N addition alone treatments (N1, N3 and N5). Thus, whereas the vegetation in the control or N addition treatments was clearly dominated by wet species, the vegetation found in the N/P addition treatments plots was characterized by more mesic species such as *Aulacomnium*, *P. arctica* and *Anthoxanthum arcticum* Veldkamp.
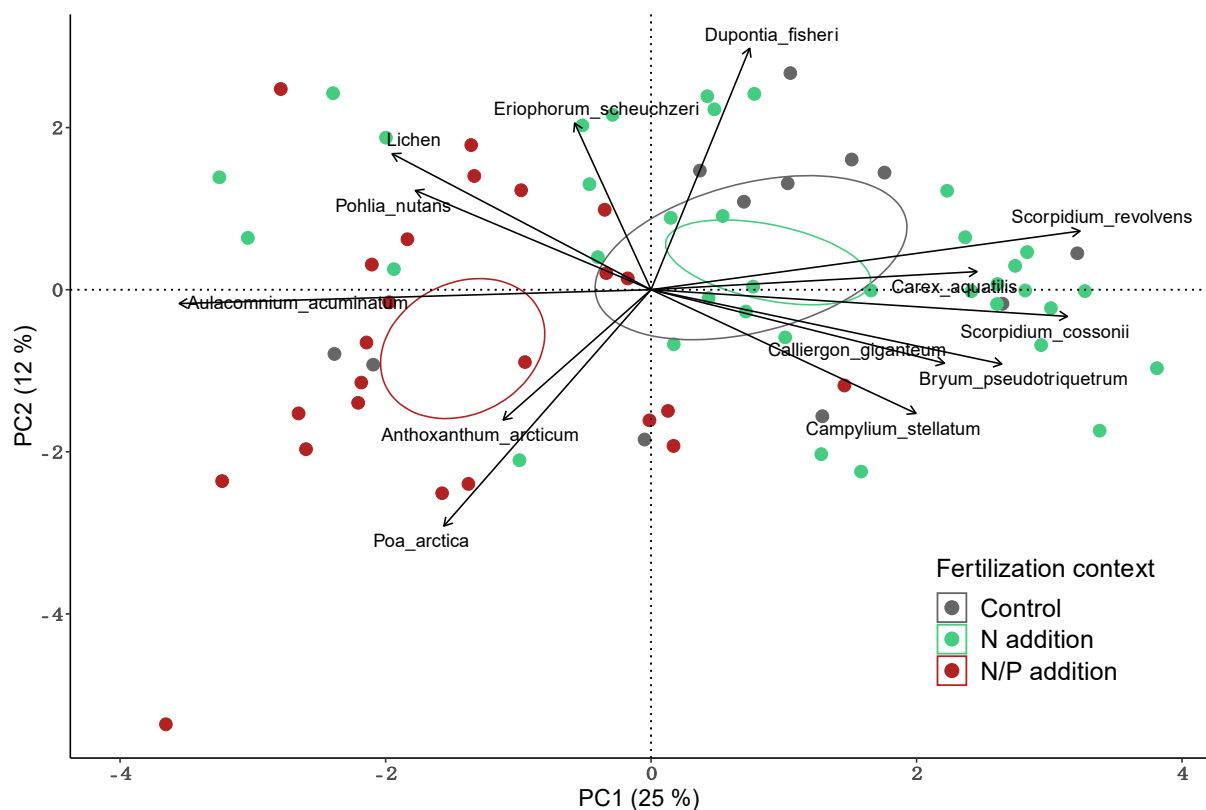


**Figure 4.** Results of the principal component analysis (PCA) on the plant composition of 72 plots with different fertilization treatments after 17 years of experimentation in tundra wetlands of Bylot Island, Nunavut. Arrows are the position of 13 plant species (seven bryophytes, five vascular plants and one lichen) most characteristic on each axis, and dots are the position of each sampled plot. The colored ellipses represent the confidence around the mean point (threshold of 0.95) of each fertilization context. The loading of plots analyzed and species contribution to the PCA are available in Tables A2 and A3, respectively.

The mean cover of *E. scheuchzeri* in the control increased by 19% between the 2nd and 17th year of experimentation (Table 3). In the N addition treatments, we noted an increase in the mean cover of *Cyperaceae* (*E. scheuchzeri* and *C. aquatilis* combined) of 21% (N5 treatment) between Year 2 and Year 17 (Table 3). In comparison, the mean cover of *Scorpidium* spp. decreased by 51% (N1 treatment) for the same period. As for N/P addition treatments, we observed an increase of 25% in the cover of *A. acuminatum* and a decrease of 59% in the cover of *Scorpidium* spp. (Table 3). No statistically significant change in the cover of

graminoid species was noted for the N/P addition treatments, largely because the shift was distributed over many species.

**Table 3.** Variation in plant species cover by vegetation strata for each fertilization treatment between year 2 and year 17 of the experiment in the tundra wetlands of Bylot Island, Nunavut). Only species with significant changes after a sequential Bonferroni correction are presented (paired *t* test, *P* < 0.00385, df = 11).

| Fertilization Context | Treatment | Strata | Species | Variation (%) | t | P |
|---|---|---|---|---|---|---|
| Control | CT | Graminoid | *Eriophorum scheuchzeri* | +18.9 | 6.4 | <0.0001 |
| N addition | N1 | Moss | *Scorpidium* spp. | −50.5 | −7.5 | <0.0001 |
| | | | *Bryum pseudotriquetrum* | −2.1 | −3.7 | 0.004 |
| | | Graminoid | *Eriophorum scheuchzeri* | +8.3 | 4.4 | 0.001 |
| | N3 | Graminoid | *Carex aquatilis* | +15.1 | 5.1 | 0.0004 |
| | N5 | Moss | *Scorpidium* spp. | −43.1 | −8.4 | <0.0001 |
| | | Graminoid | *Carex aquatilis* | +15.9 | 3.8 | 0.003 |
| | | | *Eriophorum scheuchzeri* | +26.1 | 4.0 | 0.002 |
| N/P addition | NP3 | Moss | *Aulacomnium acuminatum* | +24.5 | 4.9 | 0.0005 |
| | NP5 | Moss | *Scorpidium* spp. | −58.6 | −5.5 | 0.0002 |

No change in total moss and graminoid cover was observed between the 2nd and 5th year of the experiment for any treatment (Table 4). The total cover of mosses declined by 33% between the 5th and the 17th year in the N5 treatment (highest N addition) but graminoid cover did not change significantly (Table 4). In the NP5 treatment (highest N/P addition), total moss cover decreased by 47%, whereas the total graminoid cover increased up to 222% between the 5th and 17th year (Table 4).

**Table 4.** Variation in plant cover by vegetation strata for each fertilization treatment between year 2 and year 5, year 5 and year 17, and year 2 and year 17 of the experiment in the tundra wetlands of Bylot Island, Nunavut. Significant change in vegetation strata after sequential Bonferroni correction are indicated with an asterisk * (paired *t* test, *P* < 0.0017, df = 11).

| Fertilization Context | Treatment | Strata | Comparison | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Years 2–5 | | Years 5–17 | | Years 2–17 | |
| | | | Variation (%) | P | Variation (%) | P | Variation (%) | P |
| N addition | N5 | Moss | −7.4 | 0.1885 | −32.6 | 0.0016 * | −37.6 | 0.0003 * |
| | N5 | Graminoid | −4.9 | 0.5589 | 43.1 | 0.2033 | 36.0 | 0.2259 |
| N/P addition | NP5 | Moss | −3.4 | 0.3693 | −46.9 | <0.0001 * | −49.0 | <0.0001 * |
| | NP5 | Graminoid | −20.9 | 0.0413 | 222.3 | <0.0001 * | 155.0 | <0.0001 * |

### 3.3. Chemical Concentration

3.3.1. Fertilization Effect after 17 Years

N addition alone linearly increased the total N concentration in the tissues of graminoids from 2.0% in the control to 2.6% in the N5 treatment 17 years of fertilization (Table 5; Figure 5). N concentration did not differ between *Cyperaceae* and *Poaceae*, and this was consistent across fertilization treatments (Table 5). However, across all fertilization treatments, P concentration in *Cyperaceae* tissues was 9% higher than in *Poaceae* after 17 years (Figure 5). P concentration in *Cyperaceae* tissues remained unaffected by any of the treatments. Similarly, N addition alone linearly increased the total N concentration in moss tissues (Table 6; Figure 5). After 17 years of fertilization, N concentration of mosses increased by 17% in N1 treatment compared to the control (Figure 5). N concentration was 66% higher in mosses that received N/P addition treatments compared to the control and were 22% higher compared to N

addition treatments (Table 6; Figure 5). P concentration in mosses tissues increased by 71% in the N/P addition treatments but remained unaffected by N addition treatments, as compared to the control (Table 5; Figure 5).

**Table 5.** Results of linear mixed models evaluating the effects of (A) fertilization after 17 years, graminoid families (*Cyperaceae*, *Poaceae*) and their interaction, and (B) fertilization, time after initiation of the experiment (2, 5 and 17 years) and their interaction on the N and P concentration of graminoid plants in the tundra wetlands of Bylot Island, Nunavut. (C) A priori contrasts were also applied on fertilization effects after 17 years.

| | Nitrogen Concentration | | | Phosphorus Concentration | | |
|---|---|---|---|---|---|---|
| | *F* | *P* | df | *F* | *P* | df |
| A. Fertilization effect after 17 years | | | | | | |
| Fertilization (F) | 24.4 | <0.0001 | 5, 32 | 2.2 | 0.3332 | 5, 32 |
| Family (Fa) | 1.1 | 0.3054 | 1, 32 | 5.1 | 0.0474 | 1, 32 |
| F × Fa | 1.5 | 0.2181 | 5, 32 | 0.05 | 0.6622 | 5, 32 |
| B. Temporal effect of fertilization | | | | | | |
| Fertilization (F) | 9.1 | <0.0001 | 5, 82 | 2.8 | 0.0209 | 5, 81 |
| Time (T) | 19.8 | <0.0001 | 2, 82 | 39.9 | <0.0001 | 2, 81 |
| F × T | 2.1 | 0.0328 * | 10, 82 | 1.4 | 0.2157 | 10, 81 |
| C. Contrasts | *t* | *P* | df | *t* | *P* | df |
| Nitrogen linear | 4.2 | 0.0003 | 22 | 0.2 | 0.9 | 22 |
| Control vs. N addition [1] | 1.7 | 0.0925 | 32 | 0.4 | 0.6782 | 32 |
| Control vs. N/P addition [2] | 1.8 | 0.0742 | 32 | 1.0 | 0.3261 | 32 |
| N addition vs. N/P addition | 0.7 | 0.4739 | 32 | 2.0 | 0.0489 | 32 |

[1] N1, N3, and N5 are grouped under the term "N addition". [2] NP3 and NP5 are grouped under the term "N/P addition".
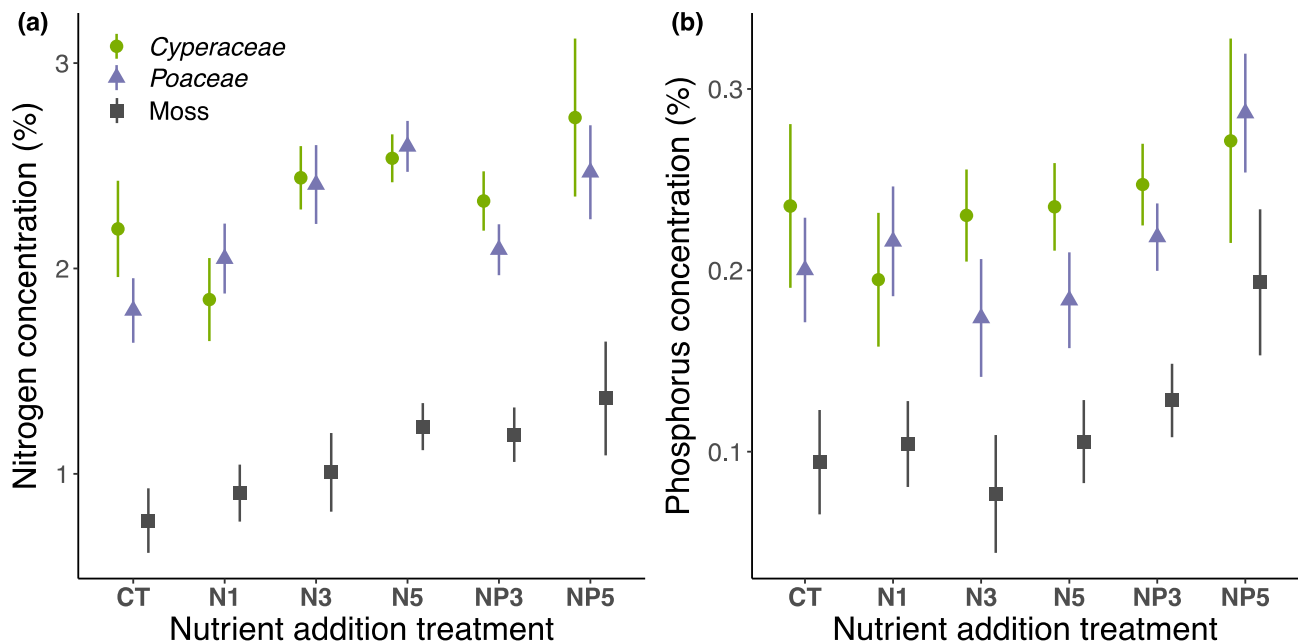


**Figure 5.** (**a**) Nitrogen concentration and (**b**) phosphorus concentration of leaves and stems according to fertilization treatments and taxonomic groups after 17 years of experimentation in the tundra wetlands at Bylot Island, Nunavut. Least square means ± SE are presented. See methods for definition of treatments.

**Table 6.** Results of linear mixed models evaluating the effects of (A) fertilization after 17 years, and (B) fertilization, time after initiation of the experiment (2, 5 and 17 years) and their interaction on the N and P concentration of mosses in the tundra wetlands of Bylot Island, Nunavut. (C) A priori contrasts were also applied on fertilization effects after 17 years.

| | Nitrogen Concentration | | | Phosphorus Concentration | | |
|---|---|---|---|---|---|---|
| | *F* | *P* | df | *F* | *P* | df |
| A. Fertilization effect after 17 years | | | | | | |
| Fertilization (F) | 9.0 | <0.0001 | 5, 19 | 16.5 | <0.0001 | 5, 19 |
| B. Temporal effect of fertilization | | | | | | |
| Fertilization (F) | 26.2 | <0.0001 | 5, 76 | 23.0 | <0.0001 | 5, 76 |
| Time (T) | 1.3 | 0.2631 | 2, 76 | 3.9 | 0.0245 | 2, 76 |
| F × T | 0.3 | 0.9665 | 10, 76 | 1.1 | 0.3894 | 10, 76 |
| C. Contrasts | *t* | *P* | df | *t* | *P* | df |
| Nitrogen linear | 3.2 | 0.0099 | 12 | 0.1 | 0.8284 | 12 |
| Control vs. N addition [1] | 1.7 | 0.0972 | 19 | 0.005 | 0.9849 | 19 |
| Control vs. N/P addition [2] | 3.1 | 0.0063 | 19 | 3.4 | 0.0028 | 19 |
| N addition vs. N/P addition | 3.4 | 0.0028 | 19 | 4.4 | 0.0003 | 19 |

[1] N1, N3, and N5 are grouped under the term "N addition". [2] NP3 and NP5 are grouped under the term "N/P addition".

### 3.3.2. Temporal Effect of Fertilization

There was a significant interaction between the effects of time and fertilization treatments on the N concentration of graminoid plants (Table 5; Figure 6). N levels after 17 years of fertilization were 21% higher on average than after 5 years in N addition treatments and 30% higher on average in N/P addition treatments, whereas no difference was observed between 5 and 2 years of fertilization (Figure 6). A significant time effect on the P concentration of graminoid plants was also observed (Table 5) as P concentration across all treatments decreased by 37% between Year 2 and 5 of fertilization and increased by 35% between Year 5 and 17 of fertilization (Figure 6). For mosses, no time effect or interaction with treatments was observed on N and P concentrations, and both were similar after 2, 5, or 17 years of fertilization (Table 6; Figure 6).
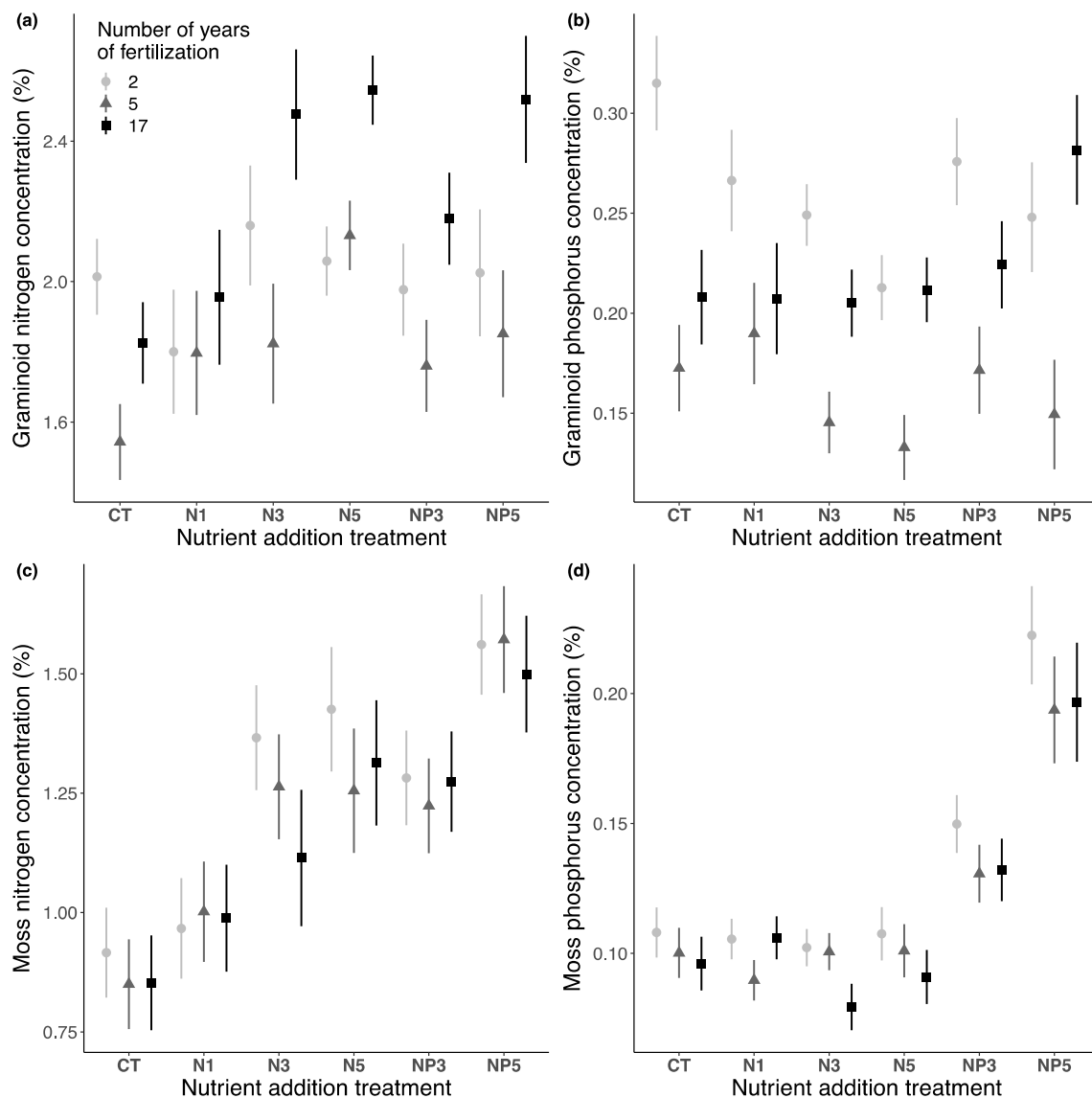
**Figure 6.** (**a**) Nitrogen concentration and (**b**) phosphorus concentration of graminoid leaves and stems, and (**c**) nitrogen concentration and (**d**) phosphorus concentration of mosses according to fertilization treatments after 2, 5, and 17 years of experimentation in the tundra wetlands at Bylot Island, Nunavut. Least square means ± SE are presented. See methods for definition of treatments.

## 4. Discussion

We simulated the anticipated increase in nutrient availability in the Arctic tundra due to increasing atmospheric N deposition in the Canadian High-Arctic [29,83] with our N addition treatments. We also simulated an overall increase in nutrient availability due to the indirect effect of global warming with our combined N/P addition treatments, as warming should lead to greater soil mineralization [64,84]. In this scenario, we assumed that most nutrients released by increased mineralization are available to the vegetation because of the high nutrient uptake capacity of graminoid plants and that losses due to run off is low. Arctic graminoid plants are known to be efficient in assimilating newly available N [85] and P [86] present in the active layer due to the high degree of vertical stratification of their root system [85]. Because precipitation levels are low in the High-Arctic, the leaching rate in these ecosystems is generally considered low as well [87]. Although the leaching rate could increase with the higher precipitation levels expected in the Arctic [28], $^{15}$N addition experiments in other tundra wetlands have shown that soil microbials can act as a significant N sink, rapidly sequestering a large proportion of available N [88,89].

Globally, N/P addition had a much stronger effect than N addition alone on primary productivity and plant composition of arctic wetlands after 17 years of experimentation. This supports our first hypothesis that global warming, through greater mineralization of organic matter and increased nutrient availability, should cause more significant changes in tundra wetland vegetation than N deposition in a system such as the Arctic, which is highly N and P co-limited [11,12]. We also observed a lag in the response time of the primary productivity of graminoid plants following fertilization. This supports our second hypothesis that the response of the vegetation to fertilization was not immediate. This suggests that mosses initially sequestered most of the nutrients and that it was probably the decomposition of the lower parts of the mosses mat that eventually allowed the graminoid plants to access the nutrients [42,43].

*4.1. Nitrogen Deposition vs. Global Warming*

After 17 years of fertilization, only the productivity of *Poaceae* was strongly increased by N/P addition treatments, whereas only the productivity of *Cyperaceae* was slightly increased by N addition treatments. This appears to be consistent with other observations [90] where after four years of N fertilization in alpine tundra, the *Cyperaceae* canopy increased by 33%, and no impact was observed for graminoids (*Poaceae*). These results suggest a differential response between *Cyperaceae* and *Poaceae* to the addition of N alone or in combination with P. It has been suggested that *Cyperaceae* benefit from added N because of their ability to use P more efficiently compared to other species [91]. *Cyperaceae* have morphological adaptations that allow them to evolve in P-poor conditions such as P acquisition through highly efficient rhizome [92]. Since the tundra ecosystem is N and P co-limited [11], *Cyperaceae* seem to have an advantage under P-poor conditions, allowing them to respond to increased N deposition while the response of other graminoids is limited. However, the competitive advantage of *Cyperaceae* over *Poaceae* weakened in the N/P addition treatments where P was no longer limited, leading to a higher productivity for *Poaceae*.

Our results suggest that moss productivity was probably also limited by P in our experiment, as mosses remained unaffected by N addition treatments, but their productivity increased slightly with N/P addition. This result is consistent with previous fertilization experiments [93,94] in rich fens where *S. cossonii* (a dominant species in our study) has been found to be mostly P limited. While N enrichment has been shown to have toxic effects on mosses due to higher $NH_4^+$ sensibility [95], P likely alleviates the negative impact of high N deposition on mosses by enhancing their capability to assimilate the deposited N [96].

Together, these results suggest that the increase in productivity of graminoids in response to warming temperatures already reported in the tundra wetlands [44] may at least in part be due to an increase in nutrient availability. Moreover, considering the much stronger response of graminoids than mosses after 17 years to our N/P addition treatments simulating the indirect effect of global warming on nutrient availability, it also shows that in the long term, a transition from moss-dominated to graminoid-dominated tundra wetlands, mainly by *Poaceae*, could be expected. This scenario had been observed in a meta-analysis [97] where long-term effects of experimental warming (mostly open-top chambers) across 61 tundra sites led to an increase in the abundance of graminoids and a decrease in moss abundance.

The treatments simulating the indirect effects of global warming on nutrient availability also influenced the floristic composition of tundra wetlands after 17 years, unlike treatments simulating N deposition only. The vegetation in the N/P addition treatments was characterized by a more mesophilic moss (*A. acuminatum*) and vascular species such as *P. arctica*. The large increase in graminoid productivity observed in the N/P addition treatments undoubtedly led to a significant increase in litter at the end of the growing season. Due to the cold conditions and slow decomposition rate, this litter was able to accumulate over time and may have favored less humid conditions and the growth of more mesophilic adapted species such as *A. acuminatum*, a moss often found on the upper edge of peat polygons. The presence of *P. arctica* in the global warming treatments may

have been favored by the high soil nutrient content, considering the small belowground biomass of this species ($4$–$15 \, \text{g m}^{-2}$) compared to other graminoid species such as *D. fisheri* ($153$–$1305 \, \text{g m}^{-2}$) or *Eriophorum vaginatum* L. ($61$–$1968 \, \text{g m}^{-2}$) [98]. In contrast, a high investment in root biomass by plant species is often considered an adaptation to increase nutrient uptake competitiveness in the context of limited soil resources [98].

The overall high and constant P concentration of *Cyperaceae* tissues across all treatments compared to *Poaceae* is consistent with the previous suggestion that *Cyperaceae* are less P sensitive than the *Poaceae* due to their species-specific physiological growth adaptations. Moreover, the linear response with N level after 17 years observed in both mosses and graminoids indicates that the plants were not saturated in N or P even at the highest doses of fertilization used. This suggests that mosses continued to absorb nutrients from the annual fertilization even after 17 years. Mosses are sensitive to nutrient addition, irrespective of age [99]. Thus, the acropetally translocation of nutrients may cause the continued nutrient absorption of mosses from older parts to newly grown segments [99].

*4.2. Lag in the Response Time*

We observed a lag in the response of graminoid productivity to the treatment simulating the indirect effect of global warming on nutrient availability since more than five years of continuous fertilization was required to reach the highest amplitude. We observed a similar lag in the increase in graminoid cover found in the highest N/P addition treatment (NP5). Mosses can act as a sponge by rapidly capturing all the nutrients added by fertilization due to their higher cation exchange capacity [100], consequently leaving less nutrients to percolate through the moss layer down to the vascular plant root level [42]. Our results support this conclusion as we observed no difference in N and P concentrations of mosses between 2, 5, and 17 years of fertilization across all treatments. This suggests a rapid and continuous absorption by mosses of nutrients added through fertilization. Graminoid plants would benefit from the nutrient addition mostly when the moss mat would start to decompose and release these nutrients a few years later. This is what we observed as, contrary to mosses, N concentration in graminoid plants exposed to fertilization increased over time and was highest after 17 years of fertilization. This could explain why the productivity of vascular plants reached its maximum only 17 years after the start of the experiment.

The N and P co-limitation in our study system could explain why we observed a lag in the productivity of graminoids only in N/P addition treatments. A meta-analysis showed that the tundra is one of the most N and P co-limited ecosystems [11]. Therefore, when the moss mat started to decompose and release its nutrients, only the graminoid plants in the plots that received both N and P additions could significantly increase their growth. Although the moss carpet also captured and sequestered N rapidly in the N addition treatments, its release following decomposition of the moss mat did not enhance graminoid growth due to the low availability of natural P. However, the lag observed in the response of graminoid productivity to the N/P addition cannot entirely reflect the real effects of global warming on nutrient availability. In our experiment, the nutrient addition occurred at the moss surface. Yet, warming should increase the availability of nutrients deeper in the soil, where the decomposition process takes place, thereby bypassing the moss absorption process that occurred in our experiment [85]. This bias derives from the experimental setup initially designed to simulate the fertilizing effects of surface-applied goose feces, which proved to be negligible [43].

Although moss productivity also responded to the treatment simulating global warming, it was weaker than in graminoids. Moreover, contrary to graminoids, no clear trend emerged regarding the temporal change in moss productivity except for particularly high productivity at Year 5 of the experiment, including in control. The bell shape of moss productivity between the 2nd, 5th, and 17th year could be explained by a decrease in productivity after 17 years due to the parallel increase in graminoids, which would reduce the resources available for mosses, primarily light. As graminoid productivity and

associated litter increased, less light was available for the lower strata, which may have reduced moss growth, as observed in a fertilization-shading experiment [32]. We also noted that in Year 5 of the experiment, when moss growth was strongest, precipitation at the beginning of the season was high (25 mm in June), and the average temperature in July was moderate (6.0 °C) (Figure A1). By contrast, Year 2 was characterized by low early season precipitation (13 mm) and a low temperature in July (4.9 °C), and Year 17 by high early season precipitation (29 mm) and a high temperature in July (13.2 °C) (Figure A1). It has been proposed that mosses are sensitive to short-term climatic conditions [101]. In general, temperature and precipitation are the two most important factors influencing the annual growth of brown mosses [102]. However, in peatland with a strong maritime influence, such as the Bylot Island tundra wetlands, a study determined that the growth of mosses was correlated more with precipitation than with temperature [103]. Nonetheless, the study emphasized a synergetic effect between these two factors because even in the presence of high rainfall during the growing season, growth will be reduced if the temperature remains cool [103]. Moreover, while there is a positive correlation between moss growth and monthly temperatures of May, June, and August, the correlation was negative in July, reflecting drought constraints [104]. Therefore, annual variation in moss productivity could be due to a short-term response to annual climatic conditions and more specifically to drought events.

Wetlands of Bylot Island are exposed to chronic grazing by geese due to the presence of a large snow goose colony [105]. Goose grazing is known to reduce primary production and change plant composition in this ecosystem [105–107]. In our study, goose grazing was suppressed since the start of our experiment, which by itself may have induced some temporal changes in plant biomass and composition in addition to those caused by fertilization and could explain some of the observed temporal changes. However, this effect is attenuated in our experiment, as we always examined the effect of the fertilization treatments in relation to a control plot where goose grazing was also suppressed. Nonetheless, we cannot exclude the possibility of a synergetic effect between goose exclusion and some fertilization treatments.

### 4.3. Limitation of the Study

A limitation of our experimental set up is that nutrients were added in a single dose, at the beginning of the growth season of plants and not continuously, unlike the enhancement of the mineralization process by global warming or atmospheric N deposition. In the latter case, however, it has been shown that atmospheric N deposition in the Arctic is dominated by episodic deposition events [108]. Although single-dose application may be a simplification, we note that the growing season of High-Arctic plants is short. Fertilizing at the beginning of the growing season, when the nutritional availability for vegetation is low [109,110], ensures that nutrients would be available when the uptake by plants is maximal. The shock treatments created by the use of a single dose should allow us to observe the maximum amplitude of the vegetation response to nutrient addition and to better understand the processes and mechanisms behind them. The lack of response that we observed in some treatments despite the relatively high doses used, such as those simulating N deposition, should further strengthen our conclusions regarding the minor role of this process in the tundra ecosystem. Finally, other factors linked to global warming, such as varying precipitation patterns and deeper or shallower snow cover, can also significantly impact vegetation growth, but these processes were not simulated by our fertilization experiment [111].

### 5. Conclusions

Our 17-year experiment shows that a sustained addition of combined N and P simulating the indirect effect of global warming had a much greater influence on the plant community of tundra wetland than N addition alone, simulating the direct effect of N deposition, a phenomenon that had not been fully demonstrated in previous short-term

studies in this environment [43,49]. Consequently, since an increase in the availability of N and P in the soil is expected with global warming, we can predict that warming is likely to have a strong impact on wetland tundra vegetation in the future. The increase in productivity and cover of graminoid plants that we observed after 17 years of fertilization mainly affected *Poaceae*, but it also altered the composition of the vegetation by favoring the growth of species characteristic of more mesic and nutrient-rich habitats. We also documented a time lag in the response of graminoid plants to an increase in soil nutrient availability up to 17 years. This lag is likely caused by the rapid nutrient uptake role of the moss mat present in this habitat, which prevents similar uptake by vascular plants. The vegetation of the tundra wetlands of the Canadian High-Arctic is therefore subject to changes under the influence of increased nutrient availability induced by global warming. Despite a latency period, a transition from a moss-dominated ecosystem to an ecosystem dominated by graminoid plants with a high proportion of *Poaceae* and eventually drier plant communities should be expected in those wetlands.

**Appendix A**

**Table A1.** List of plant species encountered during the summer 2019 inventories in the tundra wetlands of the Qarlikturvik Glacial Valley on Bylot Island (Nunavut, Canada). Nomenclature follows VASCAN [112] for vascular plants and BRYOQUEL [113] for bryophytes.

| Strata | Family | Species | Authority |
|---|---|---|---|
| Shrub | *Salicaceae* | *Salix arctica*<br>*Salix reticulata* | Pallas<br>Linnaeus |
| Graminoid | *Cyperaceae* | *Carex aquatilis*<br>*Eriophorum angustifolium*<br>*Eriophorum scheuchzerii* | Wahlenberg<br>Honckeny<br>Hoppe |

**Table A1.** *Cont.*

| Strata | Family | Species | Authority |
|---|---|---|---|
| | *Juncaceae* | *Luzula confusa* | Lindeberg |
| | | *Luzula nivalis* | (Laestadius) Sprengel |
| | *Poaceae* | *Alopecurus magellanicus* | Lamarck |
| | | *Arctagrostis latifolia* | (R. Brown) Grisebach |
| | | *Dupontia fisheri* | R. Brown |
| | | *Festuca brachyphylla* | Schultes & Schultes f |
| | | *Anthoxanthum arcticum* | Veldkamp |
| | | *Pleuropogon sabinei* | R. Brown |
| | | *Poa arctica* | R. Brown |
| Forb | *Asteraceae* | *Tephroseris palustris* | L. Reichenbach |
| | *Brassicaceae* | *Cardamine pratensis* | Linnaeus |
| | | *Draba* sp. | Linnaeus |
| | | *Eutrema edwardsii* | R. Brown |
| | *Caryophyllaceae* | *Cerastium arcticum* | Lange |
| | | *Silene uralensis subsp. uralensis* | Ruprecht Bocquet |
| | | *Stellaria longipes* | Goldie |
| | *Orobanchaceae* | *Pedicularis langsdorffii subsp. arctica* | (R. Brown) Pennell ex Hultén |
| | | *Pedicularis sudetica* | Willdenow |
| | *Saxifragaceae* | *Chrysosplenium tetrandrum* | Th. Fries |
| | | *Saxifraga cernua* | Linnaeus |
| | | *Saxifraga hirculus* | Linnaeus |
| | | *Saxifraga oppositifolia* | Linnaeus |
| Bryophytes | *Amblystegiaceae* | *Campylium stellatum* | (Hedwig) C. Jensen |
| | | *Tomenthypnum nitens* | (Hedwig) Loeske |
| | *Aneuraceae* | *Aneura pinguis* | (Linnaeus) Dumort |
| | *Aulacomniaceae* | *Aulacomnium acuminatum* | (Lindberg & Arnell) Kindberg |
| | | *Aulacomnium palustre* | (Hedwig) Schwagrichen |
| | | *Aulacomnium turgidum* | (Wahlenberg) Schwagrichen |
| | *Brachytheciaceae* | *Brachythecium turgidum* | (Hartman) Kindberg |
| | *Bryaceae* | *Bryum cryophilum* | Mårtensson |
| | | *Bryum pseudotriquetrum* | (Hedwig) Gaertner, Meyer & Scherbius |
| | *Calliergonaceae* | *Calliergon giganteum* | (Schimper) Kindberg |
| | | *Scorpidium cossonii* | (Schimper) Hedenas |
| | | *Scorpidium revolvens* | (Swartz) Rubers |
| | *Dicranaceae* | *Oncophorus wahlenbergii* | Bridel |
| | *Meesiaceae* | *Meesia triquetra* | (Linnaeus ex Jolyclerc) Ångström |
| | *Mielichhoferiaceae* | *Pohlia nutans* | (Hedwig) Lindberg |
| | *Mniaceae* | *Cinclidium arcticum* | (Bruch & Schimper) Schimper, Kongl |
| | | *Pseudobryum cinclidioides* | (Huebener) T.J. Kop. |
| | *Polytrichaceae* | *Polytrichum commune* | Hedwig |
| | | *Polytrichum swartzii* | Hartman |
| | *Sphagnaceae* | *Sphagnum* sp. | Linnaeus |

**Table A2.** Factor loading of each plot analyzed by principal component analysis (PCA). Only the first two axes are shown.

| Plot | Fertilization Context | PC1 | PC2 | Plot | Fertilization Context | PC1 | PC2 |
|------|----------------------|------|-------|------|----------------------|-------|-------|
| 1 | CT | 3.46 | 0.48 | 37 | N | 2.78 | −0.01 |
| 2 | CT | 2.94 | −0.17 | 38 | N | 0.19 | 0.02 |
| 3 | N | 3.09 | 0.37 | 39 | N | −2.18 | 0.40 |
| 4 | N | 3.27 | −0.20 | 40 | N | −0.46 | 1.38 |
| 5 | N | 3.16 | −0.85 | 41 | CT | −0.39 | −1.40 |
| 6 | N | 3.10 | −0.17 | 42 | CT | 1.36 | −1.36 |
| 7 | N | 3.55 | −0.07 | 43 | NP | −2.80 | −1.39 |
| 8 | N | 3.05 | 0.24 | 44 | NP | −2.31 | −2.03 |
| 9 | NP | 1.42 | −1.24 | 45 | NP | −2.50 | −0.67 |
| 10 | NP | −0.25 | 0.13 | 46 | NP | −2.18 | −0.21 |
| 11 | NP | −1.32 | −2.54 | 47 | N | 0.95 | 0.02 |
| 12 | NP | 0.34 | −0.02 | 48 | N | 0.39 | −0.41 |
| 13 | N | 2.67 | 0.54 | 49 | N | −0.66 | 0.64 |
| 14 | N | 2.53 | 1.07 | 50 | N | −0.22 | 1.97 |
| 15 | N | 3.52 | −1.95 | 51 | N | −0.28 | 0.27 |
| 16 | N | 3.90 | −1.03 | 52 | N | −2.01 | 1.66 |
| 17 | CT | 2.15 | 1.43 | 53 | CT | 0.87 | 2.89 |
| 18 | CT | 1.90 | 1.58 | 54 | CT | 0.82 | 1.42 |
| 19 | NP | −2.85 | −2.46 | 55 | NP | −1.12 | −0.97 |
| 20 | NP | −3.59 | −5.69 | 56 | NP | −0.84 | 1.43 |
| 21 | NP | 0.43 | −1.52 | 57 | NP | −2.91 | 2.61 |
| 22 | NP | −0.09 | −1.62 | 58 | NP | −1.75 | 1.70 |
| 23 | N | 2.60 | −0.10 | 59 | N | −0.06 | 2.52 |
| 24 | N | 2.65 | −0.02 | 60 | N | −2.42 | 2.49 |
| 25 | N | 0.53 | 0.88 | 61 | CT | −2.51 | −0.92 |
| 26 | N | 0.81 | 2.29 | 62 | CT | −2.81 | −0.72 |
| 27 | N | 0.34 | 2.39 | 63 | N | 0.86 | −0.49 |
| 28 | N | −0.80 | 2.03 | 64 | N | 1.01 | −1.99 |
| 29 | CT | 0.69 | 1.45 | 65 | N | 0.18 | −0.13 |
| 30 | CT | 0.97 | 1.12 | 66 | N | 1.35 | −0.12 |
| 31 | NP | −1.32 | 0.47 | 67 | N | 1.97 | −2.43 |
| 32 | NP | −1.55 | 0.15 | 68 | N | −0.99 | −2.09 |
| 33 | NP | −0.33 | 1.11 | 69 | NP | −0.86 | −1.58 |
| 34 | NP | −0.81 | 1.36 | 70 | NP | −2.18 | −1.97 |
| 35 | N | −3.08 | 0.53 | 71 | NP | −2.45 | −1.01 |
| 36 | N | −2.84 | 1.49 | 72 | NP | −2.58 | −1.27 |

**Table A3.** Contribution loading of each species analyzed by principal component analysis (PCA). Only the first two axes are shown. Species with the highest loadings on either side of each axis are indicated with an asterisk *.

| Species | PC1 | PC2 |
|---------|------|------|
| *Aulacomnium acuminatum* * | 0.54 * | 0.33 * |
| *Aneura pinguis* | −0.01 | 0.01 |
| *Brachythecium turgidum* | 0.04 | 0.07 |
| *Bryum pseudotriquetrum* | −0.21 | −0.10 |
| *Calliergon giganteum* | −0.11 | −0.08 |
| *Campylium stellatum* | −0.16 | −0.27 * |
| *Cinclidium arcticum* | 0.03 | −0.09 |
| *Meesia triquetra* | −0.11 | −0.11 |
| *Oncophorus wahlenbergii* | 0.00 | 0.00 |
| *Pohlia nutans* | 0.09 | 0.20 |
| *Polytrichum swartzii* | 0.08 | 0.03 |
| *Scorpidium cossonii* * | −0.40 * | −0.22 * |
| *Scorpidium revolvens* * | −0.42 * | −0.01 |
| *Sphagnum* sp. | −0.01 | 0.05 |

**Table A3.** *Cont.*

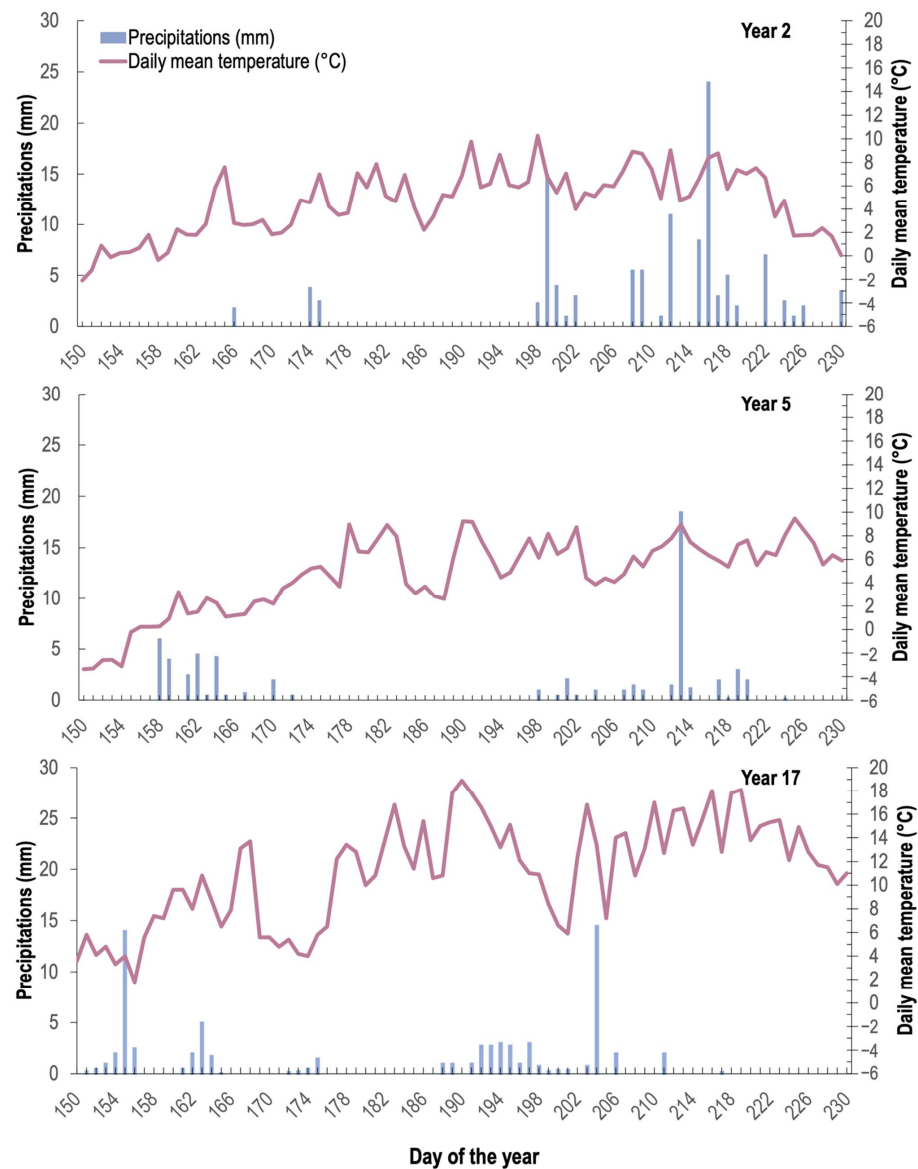| Species | PC1 | PC2 |
|---|---|---|
| *Tomenthypnum nitens* | 0.07 | −0.14 |
| Lichen * | 0.13 | 0.24 * |
| *Eriophorum scheuchzeri* * | 0.02 | 0.30 * |
| *Arctagrostis latifolia* | −0.20 | 0.09 |
| *Carex aquatilis* * | −0.25 * | 0.07 |
| *Chrysosplenium tetrandrum* | 0.01 | −0.03 |
| *Dupontia fisheri* * | −0.07 | 0.34 * |
| *Anthoxanthum arcticum* | 0.13 | −0.05 |
| *Pedicularis langsdorffii subsp. arctica* | −0.11 | 0.10 |
| *Poa arctica* * | 0.30 * | −0.72 * |
| *Draba* sp. | 0.03 | 0.03 |
| *Salix arctica* | 0.12 | 0.11 |



**Figure A1.** Precipitation (mm) and mean daily temperature (°C) for summer 2004 (Year 2), 2007 (Year 5) and 2019 (Year 16) on Bylot Island. The average daily temperature for the summer was 3.6 °C in 2004, 4.7 °C in 2007 and 11.1 °C in 2019. Cumulative precipitation for the summer was 141.5 mm over 30 rainy days in 2004, 62.7 mm over 26 rainy days in 2007 and 71.8 mm over 32 rainy in 2019 [52].

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