

Growth Rate of an Aquatic Bryophyte (*Warnstorfia fluitans* (Hedw.) Loeske) from a High Arctic Lake: Effect of Nutrient Concentration

TENNA RIIS,^{1,2} BIRGIT OLESEN,¹ CASPER K. KATBORG¹ and KIRSTEN S. CHRISTOFFERSEN³

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ABSTRACT. The High Arctic is one of the regions most susceptible to climate change on a global scale. Increased temperature, precipitation, and cloud cover are anticipated in the region, with consequent increases in nutrient runoff to surface waters. Mosses are often the dominant submerged macrophyte in Arctic and High Arctic lakes. If the growth rate of mosses in these lakes is nutrient-limited, then production could increase with climate changes that result in higher nutrient concentrations. We conducted a laboratory study to 1) measure the growth response of *Warnstorfia fluitans* (Hedw.) Loeske from a High Arctic lake to nitrogen and phosphorus availability; and 2) determine whether growth rate was N- or P-limited by examining its relationship to internal P and N content. The growth rates of *W. fluitans* were generally low, ranging from 0.003 to 0.012 day⁻¹. The growth rates increased with increasing plant P content, but not with increasing N content, indicating that moss growth was P-limited at low P availability in the experiment. Critical plant P concentration for maximum growth rate was 0.086% dry weight. This is the first time a critical P threshold has been calculated. The results imply that if climate changes result in increased P concentrations in surface waters, a higher production of moss could occur in High Arctic lakes.

Key words: High Arctic lakes, aquatic bryophytes, nutrients, growth rates, tissue nutrient, moss

RÉSUMÉ. L'Extrême arctique est l'une des régions du monde les plus susceptibles au changement climatique. La région devrait enregistrer des hausses de températures, de précipitations et de couvertures nuageuses, ce qui se traduira par des augmentations conséquentes d'écoulement des nutriments dans les eaux de surface. Dans les lacs de l'Arctique et de l'Extrême arctique, les mousses constituent souvent le macrophyte submergé prédominant. Si le taux de croissance des mousses de ces lacs est restreint par les nutriments, la production pourrait alors augmenter avec les changements climatiques qui donnent des concentrations de nutriments plus grandes. Nous avons réalisé une étude en laboratoire dans le but 1) de mesurer la réponse de croissance de *Warnstorfia fluitans* (Hedw.) Loeske d'un lac de l'Extrême arctique vis-à-vis de la disponibilité en azote et en phosphore; et 2) de déterminer si le taux de croissance était restreint par N ou par P en examinant sa relation par rapport à sa teneur interne en N et en P. Les taux de croissance de *W. fluitans* étaient généralement faibles, allant de 0,003 à 0,012 jour⁻¹. Les taux de croissance augmentaient en même temps que la teneur en N des plantes augmentait, mais pas en même temps que la teneur en P augmentait, ce qui laisse entrevoir que la croissance des mousses était restreinte par P en fonction de la faible disponibilité en P dans le cadre de l'expérience. La concentration critique en P dans les végétaux donnant lieu à un taux de croissance maximal était de 0,086 % du poids sec. Il s'agit de la première fois qu'un seuil critique de P a été calculé. Les résultats laissent entendre que si des changements climatiques se traduisent par des concentrations accrues en P dans les eaux de surface, une plus grande production de mousse pourrait se produire dans les lacs de l'Extrême arctique.

Mots clés : lacs de l'Extrême arctique, bryophytes aquatiques, nutriments, taux de croissance, nutriment dans le tissu, mousse

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INTRODUCTION

The High Arctic region is an area susceptible to large climate changes, and the main change in the coming decades will be a rise in temperature. Over the past 100 years, the average temperature has increased by 0.6°C, and an additional rise of 5°C is expected in certain areas during the next 100 years, compared to a global mean temperature rise of 2–3.5°C (Serreze et al., 2000; ACIA, 2004). Increases

in precipitation and cloud cover are also anticipated in the region (Cattle and Crossley, 1995; IPCC, 2007).

High Arctic lakes are nutrient-poor, and the greatest proportion of a lake's primary production is often from benthic mosses (Welch and Kalff, 1974). Mosses in High Arctic lakes can be found growing at great depths, even though the lakes are free of ice and snow cover for only one to three months in summer (Bodin and Nauwerck, 1968; Welch and Kalff, 1974; Priddle, 1980). The domination of mosses is

¹ Department of Biological Sciences, Aarhus University, Ole Worms Allé, Building 1135, 8000 Århus C, Denmark

² Corresponding author: tenna.riis@biology.au.dk

³ Freshwater Biological Laboratory, University of Copenhagen, Helsingørsgade 51, 3400 Hillerød, Denmark

likely a result of their adaptation to low temperatures, their low light and nutrient requirements, and their slow growth and decomposition rates (Bodin and Nauwerck, 1968; Grahn et al., 1974; Kallio and Kärenlampi, 1980; Riis and Sand-Jensen, 1997). The moss vegetation in Arctic lakes has been found to be dominated by species of the genera *Calliergon*, *Drepanocladus*, *Warnstorfia*, and *Scopidium* (Sand-Jensen et al., 1999; Hawes et al., 2002; E. Warncke, pers. comm. 2008).

The typical low nutrient concentration in High Arctic lakes means that production of mosses may be nutrient-limited during the growing season. The most common limiting nutrients in lake primary production are nitrogen (N) and phosphorus (P), which generally occur at lower concentrations than would saturate primary production. Therefore, if N and P concentrations are increased in lakes where plant growth is limited by one of these nutrients, then primary production will increase.

Future climate changes are expected to cause increasing N and P concentrations in lake waters because of increased nutrient runoff from the catchment. It has been predicted that higher summer temperatures could lead to an increase in bacterial decomposition of peat and mineralization of organic materials in the catchment (Chapin et al., 1995; Meltofte et al., 2008), as well as a release of P from melting permafrost (Hobbie et al., 1999). Precipitation in the area is expected to increase (Birks and Ammann, 2000) and in combination with increased nutrients in the runoff water it is most likely that the receiving lake will become eutrophic. One main effect of eutrophication in lakes is increased biomass of phytoplankton or filamentous green algae and consequently, lower light penetration to the submerged vegetation including aquatic mosses (e.g., Sand-Jensen and Søndergaard, 1981). The algae growth will be exacerbated by the expected increase in water temperature. Decreased light penetration will most likely lead to a decrease in the maximum depth at which submerged plants grow and possibly to the disappearance of some submerged species.

Another predicted climate change in the High Arctic is increased precipitation, including snowfall (Cattle and Crossley, 1995; IPCC, 2007). More snow on an ice-covered lake will result in lower light penetration into the lake water in spring and early summer, and it may also extend the period of ice cover by insulating the ice. The photoautotrophic organisms in the lake may therefore experience a reduced growing season along with higher nutrient availability and possibly higher temperature.

In this study we examine the effect of nutrient concentration on the growth of an aquatic moss species (*Warnstorfia fluitans* (Hedw.) Loeske) as part of predicting the effect of climate changes on moss production in High Arctic lakes. Growth experiments at different combinations of N and P concentration and analyses of internal plant N and P concentration allow us to determine if mosses are N- or P-limited and to determine the internal plant concentration of the limiting nutrient that is critical to achieve the maximum growth rate. Our study had two specific objectives:

1) to measure the response in growth rate of *W. fluitans* from a High Arctic lake to different inorganic N and P concentrations; and 2) determine whether growth rate was N- or P-limited by examining its relationship to internal P and N content. With the results, we discuss the effect of ambient nutrient concentration on plant nutrient content and evaluate how future climate changes may affect the growth rate and production of mosses in High Arctic lakes.

METHODS

W. fluitans was collected in August 2006 from a clear water lake in Peary Land, Kap Molkte, Northeast Greenland (82°10.725' N, 29°44.293' W). The lake, located 73 m asl, has a surface area of 1.65 ha and a maximum depth of about 10 m.

Water samples were taken in the middle of the water column. At the time of collection, the concentrations of total nitrogen (TN) and total phosphorus (TP), including organic N and P, in the water were 0.54 mg TN L⁻¹ and 6 µg TP L⁻¹. The TP is comparable to previous measurements of 5–10 µg TP L⁻¹ in lakes in the Zackenberg region, Northeast Greenland (Christoffersen et al., 2008). However, the TN concentration in the Zackenberg region lakes (0.2 mg TN L⁻¹) was only about half that in our study lake. The Secchi depth in the study lake was 4.25 m, and there was extensive moss coverage at depths greater than 5 m. Dissolved organic carbon was 3.2 mg L⁻¹ on the sampling day.

Moss samples were withdrawn with a rake from approximately 5 m depth and were kept chilled and in the dark until delivery (within two weeks) to the University of Aarhus, Denmark. At the university laboratory, the mosses were placed in aquariums at 4°C in a 50:50 mixture of tap water and demineralized water. The aquariums were bubbled with atmospheric air. The N and P concentrations in the aquariums were 0.6 mg NO₃⁻ L⁻¹ and 5 µg P L⁻¹. The light regime was 16:8 h at 100 µmol m⁻² s⁻¹, which is sufficient for maximum photosynthesis in mosses (Carballeira et al., 1998; Núñez-Olivera et al., 2004). The mosses were held under these conditions until the growth experiments began.

The growth rate response of *W. fluitans* to increased nutrient concentrations was studied with a multi-factorial experiment with nitrogen (N) and phosphorus (P) as independent factors. When we set up the growth experiment, we did not know the concentration of nutrients in the lake, so we chose four concentrations under the assumption of low nutrient concentrations corresponding to the earlier measurements from lakes in the Zackenberg area of Northeast Greenland (Christoffersen et al., 2008). Four concentrations of N as NH₄NO₃ (0.05 mg L⁻¹, 0.1 mg L⁻¹, 0.3 mg L⁻¹, and 1 mg L⁻¹) and P as KH₂PO₄ (2 µg L⁻¹, 5 µg L⁻¹, 15 µg L⁻¹, and 50 µg L⁻¹) were used in the experiment. All combinations of N and P concentrations were included in the experiments, with three replicates of each combination (n = 48).

Throughout the experiment, the mosses were grown in aquariums (25 × 15.5 × 16 cm; volume 6 L) with 5 L of

one-third strength Barko solution (Smart and Barko, 1985) in demineralized water containing 30.6 mg CaCl₂ L⁻¹ and 23.0 mg MgSO₄ L⁻¹ and a dissolved inorganic carbon (DIC) solution of 0.28 milli Mol (mM) (0.23 mM KHCO₃ and 0.05 mM NaHCO₃). We also added 0.1 ml L⁻¹ of a micro-nutrient solution (Tropica). The pH in the aquariums was adjusted with 1M NaOH to pH 7 and was stable throughout the experiment. The aquariums were bubbled with CO₂-enriched air to avoid carbon limitation, because CO₂ is the main carbon source for aquatic bryophytes (Bain and Proctor, 1980). The water temperature and light regime were maintained, as described above, at 4°C and 16:8 h at 100 μmol m⁻² s⁻¹. The experiment ran for four months, from October 2006 to February 2007. The aquariums were emptied and cleaned every second week to minimize microalgal growth on the mosses. The concentrations of PO₄³⁻ and NH₄⁺ were measured twice a week, and nutrients were added to maintain the original levels.

In total, 240 shoots of *W. fluitans* were distributed amongst the aquariums. All shoots had an active apical meristem and were chosen to be as morphologically similar to each other as possible. Each shoot was adjusted to a length of 6 cm, dabbed with a paper tissue, and weighed (fresh weight, FW). In each aquarium, five shoots were attached to a horizontally positioned plastic mesh with plastic-coated strips. The FW of ten other shoots was also measured, and these shoots were then freeze-dried and reweighed to give the dry weight (DW) for an initial FW/DW relationship. This relationship was used to estimate the initial DW of the shoots used in the experiment.

After 18 weeks the moss shoots were removed from the plastic mesh, and epiphytic algae were gently cleaned off with a soft brush. The five shoots from each aquarium were wrapped individually in pre-weighed aluminum foil, freeze-dried, and weighed (final DW). The growth rate of each shoot was expressed as changes in DW during the experiment and calculated as $\mu = (\ln B_t - \ln B_0) t^{-1}$, where B₀ is initial DW, B_t is final DW at time t, and t is the number of days in the experiment. The growth rate was taken to be linear, but it is not known if switching the shoots to a medium with a different nutrient regime at the beginning of the experiment caused any deviations from linearity.

The content of carbon, nitrogen, and phosphorus was measured in shoots from each treatment, as well as on a set of initial plant shoots. Since biomass was scarce, five plants were pooled for the initial analyses to obtain one value. To have sufficient plant material to conduct analyses on the treated shoots, we pooled the shoots from within each aquarium (n = 3 aquariums). Carbon and nitrogen were measured on an HCN analyzer (NA 2000 N-Protein – Fisions Instruments). Phosphorus was determined by Inductively Coupled Plasma optical emission spectrometry (ICP, Optima 2000 DV) after digestion of the freeze-dried material in HNO₃-H₂O₂ in a microwave oven (Multiwave 3000, Anton Paar GmbH, Austria).

Data Analysis

To determine the growth rate response of *W. fluitans* to nitrogen and phosphorous concentrations in the water (N_{water} and P_{water}), we first calculated mean growth rate of the shoots (n = 5) in each aquarium, and then averaged the three aquariums in each treatment (n = 3).

General linear models were used to analyze the effect of N_{water} and P_{water} on growth rates from change in weight during the experimental period and internal plant N and P content (N_{plant} and P_{plant}). We tested the variance in homogeneity by unusual residuals (± 3). The main effects were compared using multiple range tests, and the interaction between main effects was analyzed by interaction plots, using 95% Tukey HSD confidence intervals because the number of samples was the same for each effect.

To obtain an objectively derived P critical threshold with standard errors for maximum growth rate, we fitted a Michaelis-Menten equation to the relative growth rate as a function of P_{plant} using $RGR = RGR_{max} [P_{tissue}] / K_d + [P_{tissue}]$. From the equation, we determined RGR_{max} and the Michaelis-Menten constant (K_d).

RESULTS

Growth Rate Response to N and P Concentrations in Water

Growth rates in *W. fluitans* varied from 0.002 to 0.012 day⁻¹ among treatments and were highly controlled by P_{water} (Fig. 1 and Table 1). Lower growth rates were recorded at low P_{water} (2 and 5 μg L⁻¹) than at high P_{water} (15 and 50 μg L⁻¹; multiple range test, $p < 0.05$) at all concentrations of N_{water}. General linear models showed a weak interaction between N_{water} and P_{water} at intermediate concentrations of N (0.1 mg N L⁻¹) and P (5 μg L⁻¹). Although standard deviations were high within treatments, there was no difference between aquariums within treatments (ANOVA, $p > 0.05$).

Plant Nutrient Content and Growth Rate

N_{water} and P_{water} significantly affected N_{plant} (Table 1). At low P_{water} (2–5 μg L⁻¹), N_{plant} was relatively high and constant (1.6–1.7% N) irrespective of N_{water} (Fig. 2A). At high P_{water}, we found that N_{plant} increased with N_{water} from 1.0% N to 1.9% N (Fig. 2A). This difference in the effect of N_{water} on N_{plant} at low and high P_{water} was reflected in significant N and P interaction (Table 1). The initial N_{plant} was 1.15% DW, indicating that at low P_{water} the mosses accumulated N in the tissue in all N_{water} treatments, while at high P_{water} the N_{plant} accumulated only in the high N_{water} treatments (Fig. 2A).

P_{plant} was highly variable (0.05%–0.24% P) among treatments, with the highest values measured in mosses grown at high P_{water} (Fig. 2B). We observed significant effects of N_{water} and P_{water} on P_{plant} and significant interaction between these effects. For mosses grown at high P_{water}, the P_{plant} decreased with increasing N_{water}, whereas P_{plant} in mosses grown at

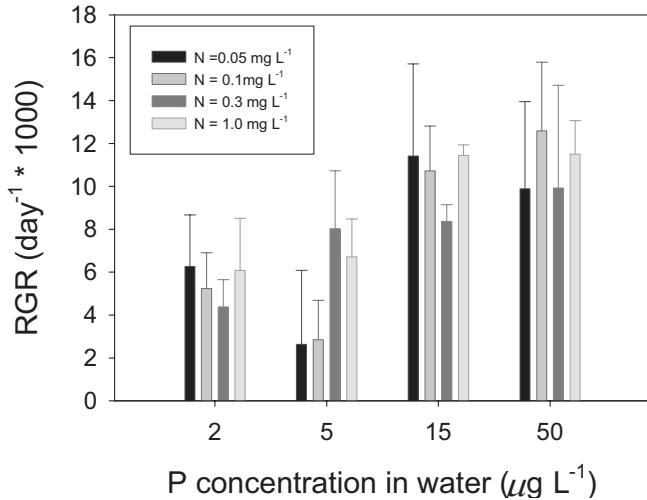


FIG. 1. Mean (\pm SD) relative growth rate (RGR) of *W. fluitans* for the three aquariums as a function of phosphorus concentration in the water (P_{water}).

lower P_{water} was unaffected by N_{water} . Thus, the N/P ratio for mosses grown at low P_{water} was two to six times as high as that for mosses grown at high P_{water} , with the greatest difference at low N_{water} (Fig. 2C). The initial P_{plant} was 0.09% DW, indicating that the mosses were using their internal pools of P at low P_{water} and were accumulating P only in the treatment with highest P_{water} and lowest P_{water} (Fig. 2B).

Carbon content in the mosses (C_{plant}) after the growth experiment varied from 41% to 47% of the total DW, and there were no significant differences among treatments (Fig. 2D, Table 1). The C/N ratio varied from 20 to 29 at low P_{water} (2 and 5 $\mu\text{g L}^{-1}$) and from 20 to 45 at high P_{water} (15 and 50 $\mu\text{g L}^{-1}$). At high P_{water} , where N_{plant} is higher, the C/N ratio decreased with increasing N_{water} (Table 1, Fig. 2E).

The C/P ratio decreased with increasing P_{water} . Its value varied from 550 to 950 at low P_{water} and from 200 to 550 at high P_{water} (Table 1, Fig. 2F). The decrease of the C/P ratio with increasing P_{water} was due mainly to increasing P_{plant} (rather than to decreasing C_{plant} , which did not vary between treatments).

Relative growth rates (RGR) are shown as a function of corresponding N_{plant} and P_{plant} in Figure 3. Fitting a Michaelis-Menten equation to the curve of RGR as a function of P_{plant} gives RGR_{max} of $0.017 \pm 0.004 \text{ d}^{-1}$ and $P = 0.082 \pm 0.043\% \text{ DW}$. On the basis of these calculations, we estimated the critical P_{plant} for 95% maximum growth rate to be $P = 0.086\% \text{ DW}$. There was no clear relationship between growth rate and N_{plant} , but there was a distinctive low RGR at intermediate N concentration in the water.

DISCUSSION

Moss Growth and Nutrient Concentrations

The plant N and P in *W. fluitans* were within the range found previously for this species in a British stream ($N = 1.2\text{--}4.2\% \text{ DW}$ and $P = 0.12\text{--}0.28\% \text{ DW}$; Ellwood and

TABLE 1. General linear model comparisons of relative growth rate (RGR), content of nitrogen, phosphorus, and carbon (% DW), and C/N, C/P, and N/P ratios in plant segments. Main effects are N and P concentrations in the water.

Dep. variable	Source	df	F-ratio	p
RGR	N	3	1.64	0.182
	P	3	39.42	< 0.001
	N \times P	9	3.47	0.001
Nitrogen content	N	3	38.25	< 0.001
	P	3	16.55	< 0.001
	N \times P	9	7.68	< 0.001
Phosphorus content	N	3	6.45	0.002
	P	3	267.48	< 0.001
	N \times P	9	8.71	< 0.001
Carbon content	N	3	0.30	0.827
	P	3	2.09	0.122
	N \times P	9	0.99	0.471
C/N ratio	N	3	15.09	< 0.001
	P	3	13.26	< 0.001
	N \times P	9	3.68	0.003
C/P ratio	N	3	0.96	< 0.001
	P	3	86.45	0.425
	N \times P	9	3.15	0.009
N/P ratio	N	3	32.52	< 0.001
	P	3	271.09	< 0.001
	N \times P	9	8.82	< 0.001

Whitton, 2007; Fig. 2) and for bryophytes in general in oligotrophic British stream systems ($N = 1.83\% \text{ DW}$ and $P = 0.10\% \text{ DW}$; Demars and Edwards, 2007). The plant tissue N and P are the nutrients intrinsically used for plant growth. Growth rates therefore reflect the tissue concentrations, and limitation of growth rates due to nutrient limitation can be interpreted from plant tissue N and P. The growth rates of *W. fluitans* increased with increasing plant P content but not with increasing N content, indicating that maximum growth rate of the moss was P-limited at low concentrations of P in the water. Based on a curve fit to the Michaelis-Menten equation, we found that critical plant P concentration for 95% maximum growth rate was 0.086% DW. Growth was impaired below this internal P content, whereas no further growth increase occurred in plants with P content above 0.086% DW. To our knowledge, no critical P value for maximum growth rate has previously been reported for aquatic bryophytes, and this value is therefore a new contribution.

There was an interactive effect of N and P in the water on plant N content, with the result that plants grown at low N and high P had lower N content in their tissue than plants grown at low N and low P. This N and P interaction supports the finding that maximum growth rate was P-limited in the experiment. The results indicate that the internal N accumulation in plants grown at low P concentrations was due to P limitation, whereas at high P availability, more N was used for growth and internal N accumulation occurred only at high N availability.

The critical plant N content below which growth rate is impaired could not be determined in this experiment.

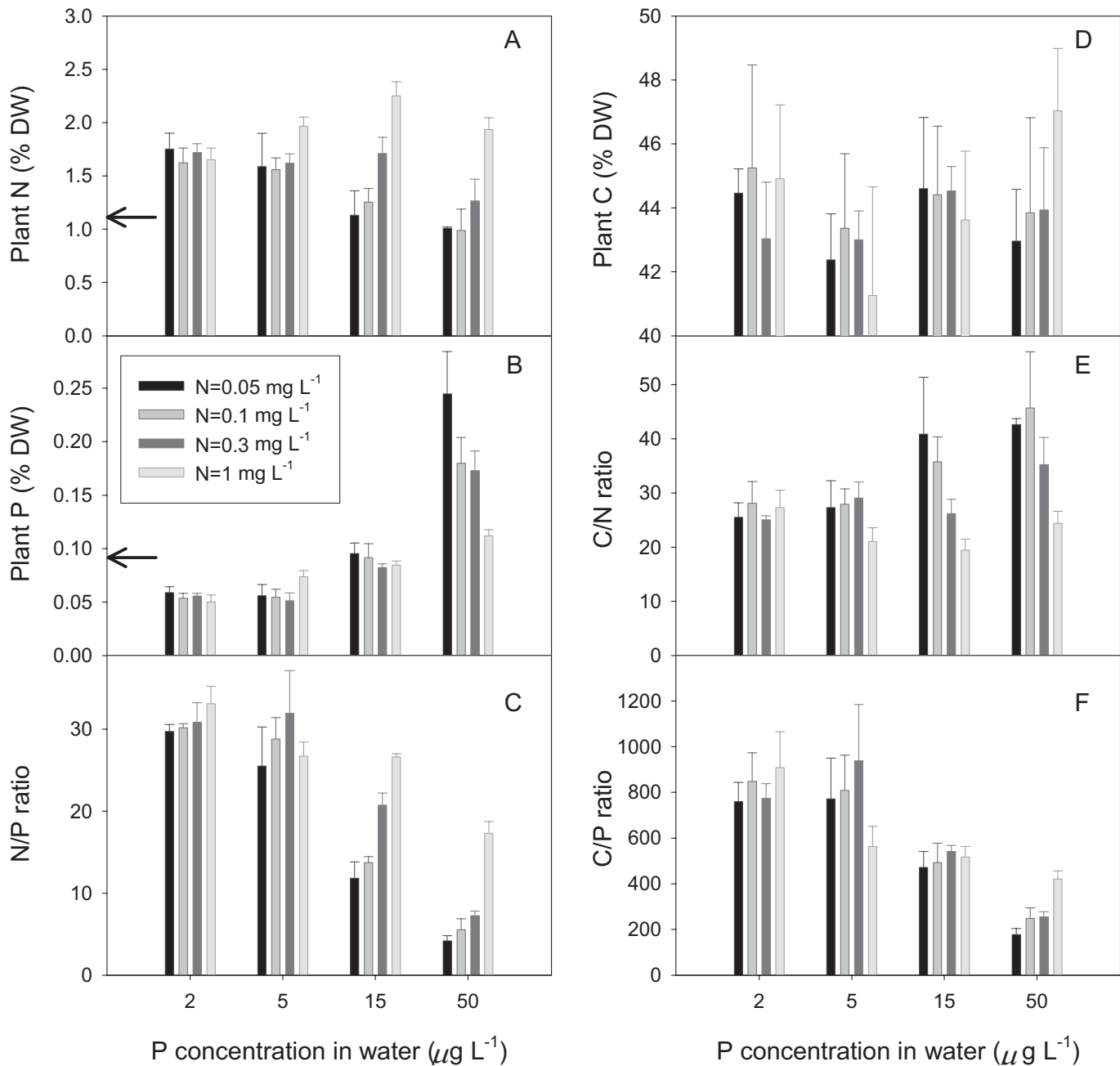


FIG. 2. Mean (\pm SD) internal plant content of nitrogen (N_{plant}), phosphorus (P_{plant}), and carbon (C_{plant}), as well as ratios of N/P, C/N, and C/P in *W. fluitans*, for the three aquariums as functions of phosphorus concentration in the water (P_{water}). Arrows indicate initial N_{plant} and P_{plant} in the moss.

Critical N values for maximum growth rate in *Sphagnum* species have been reported at 0.7% DW (Lamers et al., 2000) and 1.2% DW (Bragazza et al., 2004). In our study, all samples had internal N content higher than 1% DW and correspondingly no indications of overall N limitations for maximum growth rates. However, when assessing the results on internal P in plants grown at high P concentrations (Fig. 2B), we found a decline in plant P with increasing N in the water. This result indicates that there might be some N limitation in the plants grown at the lowest N and highest P concentrations, because P apparently accumulates in the plants instead of being used in growth. Also the N/P ratio of around 5 in the combination of high P_{water} and low

N_{water} suggests extensive N limitation compared to the findings by Duarte (1992) of a general N/P ratio of 12 in aquatic plants. Moreover, relative growth rate as a function of plant N showed that plants grown at 2 and 5 $\mu\text{g P L}^{-1}$ had a distinctive low growth rate. Of the plants grown at 5 $\mu\text{g P L}^{-1}$, those given the two treatments with low N content in the water (0.05 and 0.1 mg N L^{-1}) had the lowest growth rates (2.6 and 2.8 d^{-1}). In contrast, plants in the treatments with high N content (0.3 and 1 mg N L^{-1}) had higher growth rates of 6.7 and 8.0 d^{-1} and no change in plant N content (1.6–1.9% DW). These results indicate N limitation at low N and low P concentrations in the water.

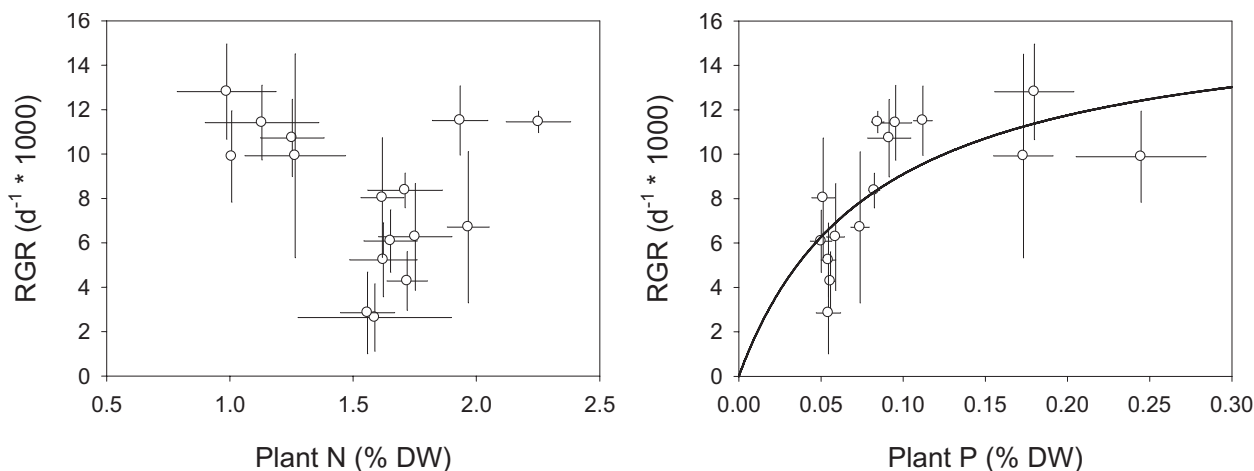


FIG. 3. Mean (\pm SD) relative growth rate (RGR) of *Warnstorfia fluitans* as a function of mean (\pm SD) internal plant content of nitrogen (N_{plant}) and phosphorus (P_{plant}). A Michaelis-Menten equation has been fitted to the RGR as a function of P_{plant} .

Consistent with our laboratory experiments are other researchers' findings that raising the available P in oligotrophic systems will positively affect moss production. Slavik et al. (2004) reviewed a long-term P enrichment experiment in the Kuparuk River in Alaska, where soluble phosphorus content was raised from around $1 \mu\text{g P L}^{-1}$ to $10 \mu\text{g P L}^{-1}$. The increased P level in the stream allowed mosses to establish and become the dominant primary producer in the system within the 15 years of the experiment (Slavik et al., 2004). Our experiment suggests that a tripling in the available P content in the lake will double the maximum growth rate and thus the production of mosses under suitable light conditions.

Moss Production and Future Climate Changes

The findings of the present study suggest that moss production will increase if climate changes result in increased nutrient concentrations in runoff to surface waters. However, many factors will influence the outcome, and increased nutrient concentrations in the water will most likely not increase growth in the same way as seen in the experiment. First, mosses often grow in dense mats rather than as single shoots. These dense mats contain higher nutrient concentrations than the surrounding water because nutrients are recycled from decaying shoots (Whitton et al., 2005), and possibly because the hydrolysis of organics by phosphatase releases phosphates, which may be dissolved in water or found as detritus (Ellwood and Whitton, 2007). Consequently, the moss might not be as P-limited as found in the experimental treatments that had water concentrations of 2 and $5 \mu\text{g P L}^{-1}$. Moreover, the growth form of mats means that only the surface individuals receive enough light to sustain maximum growth rates. Most of the moss biomass is shaded, so light limitation will prevent increased growth rates in response to higher nutrient concentrations.

Second, higher nutrient concentrations in the water would most likely increase phytoplankton production, which could affect light availability at the lake bottom.

Again, less light would limit higher moss production as a function of higher water nutrient concentrations. In a worst-case scenario, the moss community would recede as a result of light limitation.

Third, climate changes are expected to result in higher snowfall in the High Arctic and therefore less light penetration to the lake water before ice breakup in midsummer. The resulting shorter growing season might offset the effects of higher nutrient concentrations, with annual production remaining at present levels.

Fourth, future changes in nutrients and temperature in High Arctic lakes may also result in the spread of new macrophyte species to the area and changes in community composition. More southerly species that depend on higher nutrient concentrations and temperatures may be able to sustain populations in the lakes and possibly come to dominate them.

Because of the limitations of our lab experiments, a next step in better predicting the effects of climate change on moss production in High Arctic lakes would be to conduct an in situ growth experiment with the mosses. To assess the effects of changes in nutrient concentrations and light conditions arising from climate change, it will be essential to study nutrient recycling and light limitation within the moss mats in their natural environment.

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REFERENCES

ACIA. 2004. Impacts of a warming Arctic: Arctic Climate Impact Assessment. Cambridge: Cambridge University Press.

- Bain, J.T., and Proctor, M.C.F. 1980. The requirement of aquatic bryophytes for free CO₂ as an inorganic carbon source: Some experimental evidence. *New Phytologist* 86:393–400.
- Birks, H.H., and Ammann, B. 2000. Two terrestrial records of rapid climatic change during the glacial-Holocene transition (14,000–9,000 calendar years BP) from Europe. *Proceedings of the National Academy of Sciences of the United States of America* 48:1390–1394.
- Bodin, K., and Nauwerck, A. 1968. Produktionsbiologische Studien über die Moosvegetation eines klaren Gebirgssees. *Schweizerische Zeitschrift für Hydrologie* 30:318–352.
- Bragazza, L., Tahvanainen, T., Kutnar, L., Rydin, H., Limpens, J., Hájek, M., Grosvernier, P., et al. 2004. Nutritional constraints in ombrotrophic *Sphagnum* plants under increasing atmospheric nitrogen deposition in Europe. *New Phytologist* 163:609–616, doi:10.1111/j.1469-8137.2004.01154.x.
- Carballeira, A., Diaz, S., Vasquez, M.D., and Lopez, J. 1998. Inertia and resilience in the responses of the aquatic bryophyte *Fontinalis antipyretica* Hedw. to thermal stress. *Archives of Environmental Contamination and Toxicology* 34:343–349.
- Cattle, H., and Crossley, J. 1995. Modeling Arctic climate-change. *Philosophical Transactions of the Royal Society of London Series* 352:201–213.
- Chapin, F.S., III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., and Laundre, J.A. 1995. Responses of Arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711.
- Christoffersen, K.S., Amsinck, S.L., Landkildehus, F., Lauridsen, T.L., and Jeppesen, E. 2008. Lake flora and fauna in relation to ice-melt, water temperature and chemistry at Zackenberg. In: Meltøfte, H., Christensen, T., Elberling, B., Forchhammer, M., and Rasch, M., eds. *High-Arctic ecosystem dynamics in a changing climate. Advances in Ecological Research* 40. New York: Academic Press. 371–389.
- Demars, B.O.L., and Edwards, A.C. 2007. Tissue nutrient concentrations in freshwater aquatic macrophytes: High inter-taxon differences and low phenotypic response to nutrient supply. *Freshwater Biology* 52:2073–2086.
- Duarte, C.M. 1992. Nutrient concentration of aquatic plants: Patterns across species. *Limnology and Oceanography* 37: 882–889.
- Ellwood, N.T.W., and Whitton, B.A. 2007. Phosphatase activities of the aquatic moss *Warnstorfia fluitans* (Hedw.) Loeske from an acidic stream in North-East England. *Hydrobiologia* 575:95–107, doi:10.1007/s10750-006-0283-0.
- Grahn, O., Hultberg, H., and Landner, L. 1974. Oligotrophication: A self-accelerating process in lakes subjected to excessive supply of acid substances. *Ambio* 3:93–94.
- Hawes, I., Andersen, D.T., and Pollard, W.H. 2002. Submerged aquatic bryophytes in Colour Lake, a naturally acidic polar lake with occasional year-round ice-cover. *Arctic* 55:380–388.
- Hobbie, J.E., Peterson, B.J., Bettez, N., Deegan, L., O'Brien, W.J., Kling, G.W., Kipphut, G.W., Bowden, W.B., and Hershey, A.E. 1999. Impact of global climate change on the biochemistry and ecology of an Arctic freshwater system. *Polar Research* 18:207–214.
- IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate change 2007: The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge and New York: Cambridge University Press.
- Kallio, P., and Kärenlampi, L. 1980. Photosynthesis in mosses and lichens. In: Cooper, J.P., ed. *Photosynthesis in different environments*. Cambridge: Cambridge University Press. 393–423.
- Lamers, L.P.M., Bobbink, R., and Roelofs, J.G.M. 2000. Natural nitrogen filter fails in polluted raised bogs. *Global Change Biology* 6:583–586.
- Meltøfte, H., Christensen, T., Elberling, B., Forchhammer, M., and Rasch, M., eds. 2008. *High-Arctic ecosystem dynamics in a changing climate: Ten years of monitoring and research at Zackenberg Research Station, Northeast Greenland. Advances in Ecological Research* 40. New York: Academic Press. 596 p.
- Núñez-Olivera, E., Martínez-Abaigar, J., Tomas, R., Beaucourt, N., and Arroniz-Crespo, M. 2004. Influence of temperature on the effects of artificially enhanced UV-B radiation on aquatic bryophytes under laboratory conditions. *Phytosynthetica* 42:201–212.
- Priddle, J. 1980. The production ecology of benthic plants in some Antarctic lakes. I. In situ production studies. *Journal of Ecology* 68:141–153.
- Riis, T., and Sand-Jensen, K. 1997. Growth reconstruction and photosynthesis of aquatic mosses: Influence of light, temperature and carbon dioxide at depth. *Journal of Ecology* 85:359–372.
- Sand-Jensen, K., and Søndergaard, M. 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 66: 529–552.
- Sand-Jensen, K., Riis, T., Markager, S., and Vincent, W.F. 1999. Slow growth and decomposition of mosses in Arctic lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 388–393.
- Serreze, M.C., Walsh, J.E., Chapin, F.S., III, Osterkamp, T., Dyrgerov, M., Romanovsky, V., Oechel, W.C., Morison, J., Zhang, T., and Barry, R.G. 2000. Observational evidence of recent change in the northern high-latitude environment. *Climate Change* 46:159–207.
- Slavik, K., Peterson, B.J., Deegan, L.A., Bowden, W.B., Hershey, A.E., and Hobbie, J.E. 2004. Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. *Ecology* 85:939–954.
- Smart, R.M., and Barko, J.W. 1985. Laboratory culture of submersed freshwater macrophytes on natural sediments. *Aquatic Botany* 21:251–263.
- Welch, H.E., and Kalff, J. 1974. Benthic photosynthesis and respiration in Char Lake. *Journal of the Fisheries Research Board of Canada* 31:609–620.
- Whitton, B.A., Al-Shehri, A.M., Ellwood, N.T.W., and Turner, B.L. 2005. Ecological aspects of phosphatase activity in cyanobacteria, eukaryotic algae and bryophytes. In: Turner, B.L., Frossard, E., and Baldwin, D.S., eds. *Organic phosphorus in the environment*. Wallingford, United Kingdom: CAB International. 205–241.