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Research Letter

Do Nitrogen Concentration and Forage Quality of the Moss *Racomitrium lanuginosum* Increase with Latitude?

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Mosses are an important component of high latitude ecosystems, contributing the majority of the plant biomass in many communities. In Arctic regions mosses also form a substantial part of the diet of many herbivore species. This may reflect either the availability of moss or its quality as forage. Here we test whether the nitrogen concentration and forage quality of the moss *Racomitrium lanuginosum* increase with latitude and discuss the findings with reference to herbivore utilisation of moss in the Arctic. In contrast to vascular plants, moss nitrogen concentration significantly decreased with latitude ($P < .01$), in line with estimates of N deposition at the sampling sites. In addition, no evidence of an increase in nutritional quality of moss with latitude was observed; thus, this study suggests that the utilisation of moss by herbivores in arctic ecosystems maybe a function of their relatively high biomass rather than their quality as forage.

1. Introduction

The concentration of nitrogen (N) in vascular plants is observed to increase with latitude [1, 2], with arctic vascular plants having higher N concentrations than those from temperate areas [3]. Whether the same trend of increasing N with latitude is also apparent in bryophytes is unknown. In high latitude ecosystems, bryophytes constitute a large component of biomass and diversity within plant communities [4]. Whilst moss is generally not a common part of vertebrate herbivore diets, it is consumed by many herbivores in the Arctic, including geese, reindeer, and rodents, contributing over 50% of the diet in some species (e.g., [5–7]). Here we test the hypothesis that moss follows the same latitudinal gradient in N concentration as vascular plants and ask whether herbivore utilisation of moss in the high Arctic is thus a reflection of its nutritional quality.

Vascular plants take up N from the soil through their roots and symbioses with fungi; however, mosses lack these adaptations and take up N principally from aboveground sources such as wet deposition, although smaller amounts are taken up from the soil [8, 9]. Thus whilst vascular plant N concentration is linked to soil N availability, moss N concentration is associated with atmospheric N deposition [10, 11]. N deposition levels are lower in the Arctic than in heavily industrialised areas including northern Europe [12]; thus, a decrease in N concentration of moss in relation to latitude may be expected. However, despite soil available N being limited by temperature and decomposition rates in high latitude systems, vascular plant N concentration are highest in these areas. This may be driven by increasing concentrations of intracellular compounds in response to abiotic conditions at high latitudes such as prevailing low temperature, low light, and a short growing season [2, 3]. Despite limiting N supply, moss N concentration may therefore increase at high latitude, due to physiological responses to abiotic conditions, in common with vascular plants.

N is a key nutrient for foraging herbivores, reflecting plant quality and being associated with herbivore selectivity [13, 14]. In this study we address whether moss follows the same pattern of increasing N concentration with latitude as

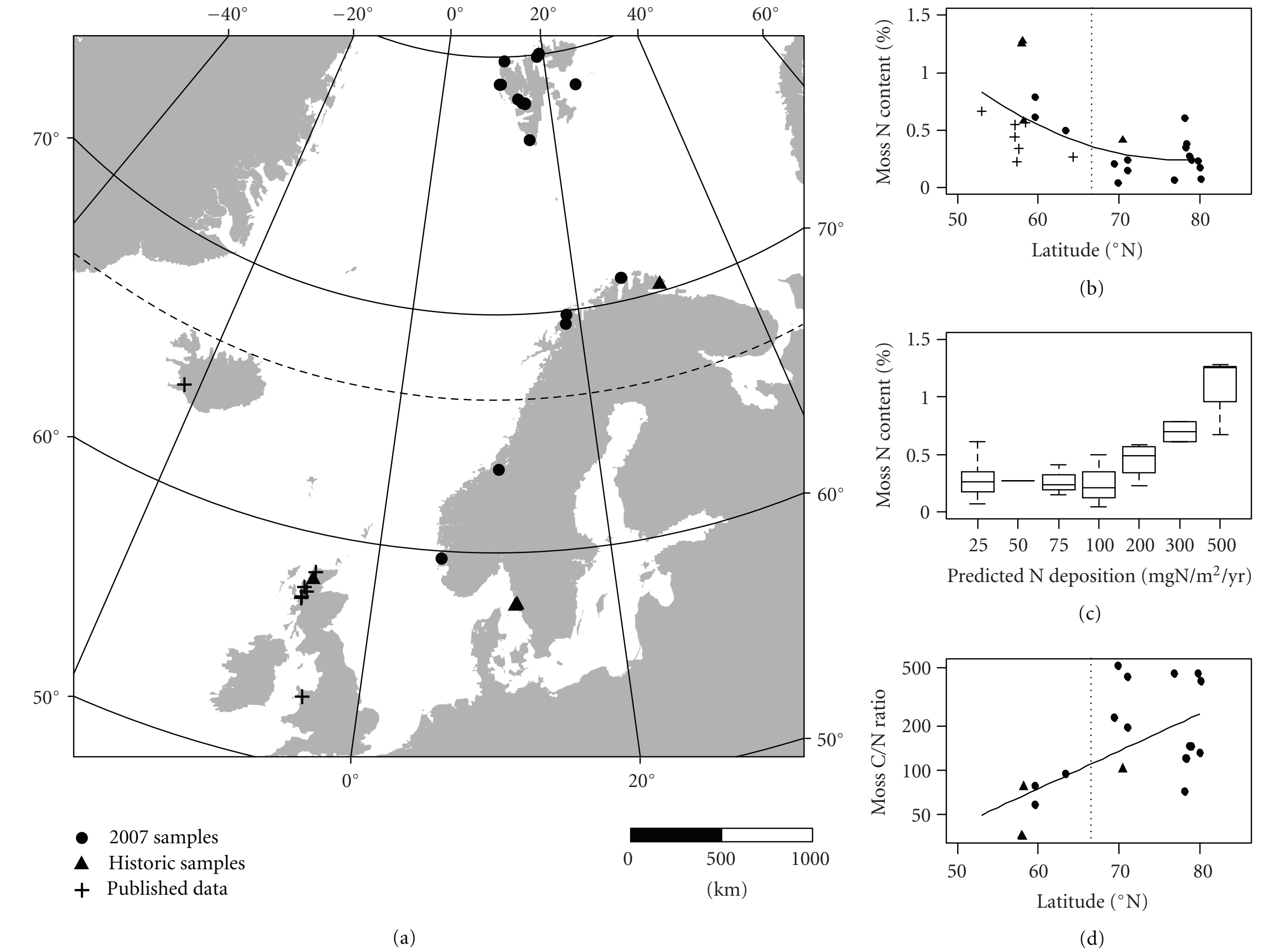

Figure 1: (a) Map showing locations of sample sites and published material. (b) Moss % N concentration plotted against latitude. Polynomial regression line; $R^2 = 36.1\%$, $n = 27$, $P < .01$. (c) Box plots showing median interquartile range and 95% confidence intervals of moss % N grouped against predicted regional N deposition derrived from model predictions [12]. (d) C/N ratio (log axis) of moss plotted against latitude. Regression line; $R^2 = 36.0\%$, $n = 20$, $P < .01$. In (a), (b) and (d), circles represent 2007 samples, triangles samples from 1990s, and crosses published material (C/N data not available in published material). The dashed line at 66.56° represents the latitude of the Arctic Circle.

vascular plants, or whether moss N concentration decreases in arctic regions reflecting lower rates of atmospheric N deposition. In order to increase understanding of herbivore utilisation of moss in arctic regions, other indicators of moss nutritional quality, including fibre concentration and C/N ratio, are also analysed.

2. Methods

The study focused on the moss *Racomitrium lanuginosum* (Hedw.) Brid. due to its latitudinal spread in distribution. *R. lanuginosum* was collected from sites on a latitudinal gradient from temperate south-west Norway to the high arctic archipelago of Svalbard during the summer of 2007. Further *R. lanuginosum* samples collected during the 1990s and stored at the University of Aberdeen, UK, were also analysed and N concentration data were collated from published literature in order to increase the spatial scale of the study (Figure 1(a)). Due to increasing moss N concentration with altitude [15], samples and published data were obtained from the lowest altitude available, with an upper limit of 500 m. When altitude was not given in published material, it was derived from the terrain model of Google Earth 4.2 (2007) from reported coordinates or locations.

To further evaluate nutritional quality of moss as herbivore food item over a latitudinal range, the carbon to N ratio, and fibre content of moss samples were also determined. These relate to structural carbohydrate content, including cellulose, hemicelluloses, and lignin content, and are inversely correlated with digestibility of plant material [16, 17].

Moss samples were oven dried, and the top 2 cm of shoots selected for analysis [11] to reflect recent growth. Samples were ground by ball mill and analysed for N and C concentration on a Fisons NA1500 NCS elemental analyser. As with Pitcairn et al. [10], we assumed that the

N concentration of stored samples would not have changed, although some decrease in C content may have occurred. The neutral detergent fibre (NDF), acid detergent fibre (ADF), and lignin constituents of moss samples were determined following the procedure of van Soest [18]. At each location, between one and four samples of moss were taken. These were analysed separately for C and N concentration and the mean value per location used, whilst material was pooled for fibre analysis to ensure sufficient quantities for analysis. Data were analysed in R 2.6.2 (R Development Core Team 2008). N concentration, C/N ratio, and fibre content were related to the latitude of sample location. Polynomial models were applied where these significantly improved the relationship. Furthermore, moss N concentration was plotted against predicted N deposition over the study region (from global models of predicted N deposition [12]) in order to better understand patterns in latitudinal patterns in moss tissue N content. Due to uncertain accuracy in the predicted N deposition across the study region and limited spatial resolution, the association between N content and deposition was not tested statistically.

3. Results

A decrease in N concentration of *R. lanuginosum* with latitude was observed (Figure 1(b); quadratic regression: $R^2 = 36.1\%$, $n = 27$, $P < .01$), with an average N concentration ($\pm$ standard error of the mean) of $0.62\% \pm 0.09$ below the Arctic Circle and $0.25\% \pm 0.04$ above the Arctic Circle. The highest N concentration was found in samples taken from southern Sweden in 1994 (Figure 1(b)). The *R. lanuginosum* samples with the highest N concentration were found to come from areas with higher predicted N deposition, with N concentration increasing when N deposition exceeded 100 mg N $m^{-2}yr^{-1}$ (Figure 1(c)). Coupled with the latitudinal decrease in N concentration in *R. lanuginosum*, the C/N increased (Figure 1(d); linear regression: $R^2 = 36.0\%$, $n = 20$, $P < .01$) with the average C/N ($\pm$ standard error of the mean) being 253.8 ± 43.6 above the Arctic Circle and 63.3 ± 10.5 below the Arctic Circle. ADF, NDF, and lignin content of *R. lanuginosum* were all unrelated to latitude ($P \geq .4$), neither were they strongly associated with N concentration ($|r| \leq 0.25$).

4. Discussion

4.1. N Gradient. The N concentration of *R. lanuginosum* shoots showed a clear decrease with increasing latitude, with higher N concentrations in temperate areas than in the Arctic. *R. lanuginosum* N concentration increased when predicted N deposition was greater than 100 mg m^{-2} yr^{-1}, levels which are found in the south of the study's latitudinal range [12]. This is an extension of the findings of Pitcairn et al. [10], that moss N is related to N deposition across the UK. Thus, whilst vascular plant N concentration may be explained by physiological responses to the low temperatures and short growing seasons that characterise both high altitude and latitude systems [1, 2], patterns of moss N concentration maybe better explained by N deposition, due to moss N uptake largely being from wet deposition [8, 9]. The observations in this study are supported by evidence in literature showing that the tissue N concentration of ectohydric mosses is related to enhanced N deposition at high altitude sites in the UK [15, 19].

The predicted N deposition values are taken from that modelled by Dentener et al. [12]. Whilst the predictions are of low resolution across the study range, preventing statistical testing of the association with moss N content, the estimates do appear consistent with other estimates from the high Arctic (e.g., [20]). Variation in moss N concentration not explained by latitude or regional predicted N deposition is thus likely to be due to local variation in N deposition. Of the Svalbard samples, the highest N concentration was found in moss from the central region close to the main settlements and mining activity; and indeed these sources are known to contribute to local atmospheric N pollution [21]. Although this study used moss material from different sources, a clear pattern is still apparent, and it remains that if just 2007 samples are used, thus we assume that the findings are robust.

4.2. Herbivory. Our study clearly shows that the dietary utilisation of moss by arctic herbivores cannot be explained by the nutritional quality of the moss as measured indicators of moss nutritional quality in the Arctic were lower than (N content and C/N ratio) or the same as (fibre content) moss from temperate regions. There was also no evidence that the limited N present in high latitude moss is more readily extractable during digestion, as fibre content was constant with latitude, and there was no association between N concentration and fibre content. Thus, there is no evidence that the forage quality of *R. lanuginosum* increases from temperate to arctic latitudes. Although *R. lanuginosum* is not a key arctic forage species itself, we suggest that due to the sensitivity of bryophytes to N deposition (e.g., [10, 22]), this pattern is likely to be consistent across many ectohydric moss species. However, it remains to be seen whether the N concentration of other bryophytes also varies with atmospheric deposition levels in the arctic. Further studies are therefore recommended using moss species that are key arctic forage plants.

In high latitude systems, herbivores may select forage on the basis of biomass rather than nutritional quality [23]. Moss is a dominant constituent of biomass within arctic vegetation communities [4]. Thus, due to the lack of an increase in nutritional quality of moss with latitude demonstrated in the current study, we suggest that the utilisation of mosses in the arctic by a range of vertebrate herbivores is best explained by its high biomass and availability within vegetation, coupled with the immediate energy demand of arctic herbivores required for survival [24].

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