

Increased Rainfall Ameliorates the Negative Effect of Trampling on the Growth of High Arctic Forage Lichens

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Abstract

Recolonisation of trampled lichen pastures in the High Arctic is dependent on the regrowth from small fragments of lichen thalli. Intact lichens have been shown to grow most rapidly during periods of sustained moisture caused by rainfall or cloudy days. Climate change models for Arctic areas predict wetter summers, milder winters and greater stochastic variability. Therefore we hypothesised that the growth of both damaged and intact Svalbard reindeer forage lichens would be increased under the future climatic scenarios. The effects of rainfall frequency, increased precipitation, and simulated cloud cover on relative growth rate (RGR) of *Cetraria delisei*, *C. islandica* and *C. nivalis*, from NW Svalbard were examined under controlled conditions. Low light did not depress RGR, suggesting that shading provided by increased cloud cover would not affect the lichen growth. The ability to gain mass and the RGR was lower in cut thalli than intact thalli under most watering regimes. Frequency of watering was the most important factor influencing

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growth, but this also interacted synergistically with quantity. Damaged thalli watered frequently grew significantly more than intact thalli watered less frequently. These results suggest that an increase in summer precipitation as predicted by climate modelling would increase the growth rate of fragmented thalli and may help to ameliorate the damage done to the lichen thalli by reindeer trampling and grazing.

Keywords: *Cetraria*, lichens, relative growth rates, climate change, Arctic, trampling, reindeer, *Rangifer* spp.

1. Introduction

Lichens are sensitive to trampling, especially when they are dry (Bayfield et al., 1981). Field observations show that much of the previously rich lichen cover of Brøggerhalvøya (Brattbakk, 1986), a peninsula of north-western Svalbard (78°60'N, 12°0'E), has been removed or damaged. This is probably due to the trampling and grazing by an exponentially increasing population of non-migratory Svalbard reindeer, *Rangifer tarandus platyrhynchus* (Cooper and Wookey, 2001; Ditlefsen, 2000). In many parts of the peninsula only small fragments of lichen thalli remain (E.J. Cooper, unpublished data), and these are susceptible to removal by wind.

Models for Arctic areas predict wetter summers, milder winters and greater stochastic variability (Intergovernmental Panel on Climate Change, 1995, Kattenberg et al., 1996; Førland and Hanssen-Bauer, 2000). Svalbard is a High Arctic archipelago (74–81°N), with relatively low annual rainfall (100–300 mm). Thus these predicted climatic changes are likely to have profound effects on the growth of vegetation, especially of fruticose lichens, important forage for Svalbard reindeer. Lichens in other regions grow most rapidly during periods of sustained moisture caused by rainfall or cloudy days (Kärenlampi, 1971; Armstrong, 1973). We hypothesised that growth of damaged lichen thalli could be increased in future conditions of greater and more frequent rainfall. We also wanted to determine the relative importance of frequency and quantity of precipitation.

We aimed to quantify the growth rates of the lichen fragments and to compare them with the growth rates of intact thalli. Further we wished to investigate whether change of some climatic parameters as predicted by global climate models would affect the lichens growth rates. A comparative laboratory study was therefore established to examine the effect of increased precipitation and frequency of rainfall events and simulated cloud cover, on the growth rates of damaged and intact lichen thalli of three lichen species from Svalbard.

2. Method

Species and collection site

Samples of three different lichen species, *Cetraria nivalis* (L.) Ach., *Cetraria islandica* (L.) Ach., *Cetraria delisei* (Bory) Th. Fr. (nomenclature follows Thomson, 1984) were collected from Brøggerhalvøya and Sarsøyra, north-western Svalbard, and brought to the phytotron at Tromsø University, in northern Norway. The phytotron consists of a number of growth rooms with closely controlled temperature, humidity and light.

Experimental design

Experiment 1.

We examined the effect of four different variables, in factorial combination, on the growth rates of the three lichen species. We compared intact thalli to those that we cut to simulate trampling. We looked at the effect on the growth rate of thalli at two different light levels, two frequencies of precipitation and two quantities of water. The treatments are summarised in Table 1.

Intact thalli of about 1.5 g wet mass and length of 3 cm for *Cetraria delisei* and 4 cm for *C. nivalis* and *C. islandica* were used for the experiment, half of which were cut 5 times to simulate reindeer trampling (treatment codes used in future reference: C = cut thalli, N = intact thalli). The lichens were air-dried for 24–36 hours and weighed. Three 'dummy' thalli were used to determine the air-dry: oven-dry mass ratio, for the estimation of the oven-dry mass of all of the test thalli (Jónsdóttir et al., 1999). The test thalli were placed in nylon netting on a bed of moss in plastic pots of 5 cm in diameter and put into a growth room of the Tromsø University phytotron at 6°C, 40% relative humidity and continual daylight to simulate a Svalbard summer growing season. The lichen was watered regularly with a fine spray of tap water of pH 7.

Treatments

Quantity of water given was either a daily average of 1 mm (given the code 'A-' in future references) or 1.5 mm ('A+'). The average daily summer precipitation of 1 mm for Ny Ålesund, was calculated from Norwegian Meteorological Office data for the period 16 June – 15 September, 1989–1998.

Frequency of watering was either; once (F-) or three times (F+) a week.

Light level used was either 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 'low light'; or 300–450 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 'high light'. The high light level was representative of a typical summer's day in Svalbard (Cooper, 1996) and should provide saturating light for the lichens (Demmig-Adams et al., 1990) and the low light level was chosen to simulate a very cloudy day. The lichens were placed on a tray

Table 1. Codes for the treatments carried out on the lichen in experiment 1. These were carried out in 'low light', $90 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ and 'high light', $300\text{--}450 \mu\text{mol.m}^{-2}.\text{s}^{-1}$.

Treatment code	Lichen	Calculated daily quantity (A) of water given (mm)	Frequency (F) of watering (weekly)
1 CA-F+	Cut	1	3
2 NA-F+	Intact	1	3
3 CA+F+	Cut	1.5	3
4 NA+F+	Intact	1.5	3
5 CA-F-	Cut	1	1
6 NA-F-	Intact	1	1
7 CA+F-	Cut	1.5	1
8 NA+F-	Intact	1.5	1

Table 2. The number of replicates of each treatment (n), the number (ng) and percentage (%) which gained mass.

Treatment	<i>Cetraria delisei</i>			<i>Cetraria islandica</i>			<i>Cetraria nivalis</i>		
	n	ng	%	n	ng	%	n	ng	%
Low light									
CA-F+	22	19	86	22	19	86	15	10	67
NA-F+	22	22	100	22	20	91	16	16	100
CA+F+	22	21	95	22	22	100	15	15	100
NA+F+	22	22	100	22	22	100	16	16	100
CA-F-	22	18	82	22	8	37	15	11	73
NA-F-	22	19	86	22	12	55	16	8	50
CA+F-	22	2	9	22	1	5	15	7	47
NA+F-	22	11	50	22	11	50	15	15	100
High light									
CA-F+	15	14	93	16	12	75	9	5	56
NA-F+	16	16	100	16	14	88	10	10	100
CA+F+	16	16	100	16	15	94	9	9	100
NA+F+	16	16	100	16	15	94	10	10	100
CA-F-	16	16	100	16	15	94	9	6	67
NA-F-	16	16	100	16	15	94	10	10	100
CA+F-	16	11	69	16	14	88	9	9	100
NA+F-	16	16	100	16	15	94	9	9	100

arranged at random in the growth room. The trays were moved clockwise in the growth room twice a week to ensure they received a comparable light flux throughout the whole experiment.

After 12 weeks, the lichens were air-dried, reweighed and the growth rates were determined. The relative growth rate (RGR) serves as a fundamental measure of dry matter production (Beadle, 1985).

Experiment 2

A second experiment on cut and intact thalli was conducted as above, but for a shorter growing period of 4 weeks. In this case, all the thalli were watered twice daily (F++), and the quantity of water used represented either 3 (A++) or 5 times (A+++) the average daily summer precipitation at Ny Ålesund. This experiment was only carried out at the high light level, but all other growth conditions were identical to experiment 1.

Data analysis

Multivariate analyses of variance were carried out on the RGR of the lichen. The parameters tested were species, cut vs. intact, light level, quantity of water and frequency of watering.

To examine for the amelioration effect of increased water on lichen growth, the RGR of intact thalli at a set frequency of watering were compared (using *t*-tests) to those of cut thalli receiving an increased quantity of water. Likewise, while keeping the quantity of water the same, intact thalli RGR were compared to those of cut thalli that received a higher frequency of watering.

Relative growth rate calculation

RGR was calculated as $(\ln W_2 - \ln W_1) / (t_2 - t_1)$ where W_1 and W_2 are initial mass and final mass, respectively, and t_1 is initial time and t_2 is the time of the final harvest. In the case of experiment 1, $(t_2 - t_1) = 12$ weeks, and for experiment 2 it was 4 weeks.

3. Results

Experiment 1

Table 2 shows the number and percentage of lichen thalli that increased in mass during the experimental period. 33% of the treatments of intact lichens had a lower percentage of thalli with a mass increase at low light compared to

Table 3. Summary statistics of multivariate analysis of variance of lichen relative growth rates. The parameters tested are: S = species, C = cut, L = light level, A = quantity of water, and F = frequency of watering.

Treatment	df	F	P	Significance
S	2	26.10	< 0.0000	***
C	1	28.78	< 0.0000	***
A	1	28.84	< 0.0000	***
F	1	166.97	< 0.0000	***
S×C	2	4.76	0.0089	**
S×A	2	12.80	< 0.0000	***
S×F	2	9.35	0.0001	***
C×A	1	4.74	0.0298	*
C×L	1	4.55	0.0334	*
A×L	1	10.30	0.0014	**
A×F	1	35.06	< 0.0000	***
F×L	1	54.28	< 0.0000	***
S×C×A	2	3.10	0.0455	*
S×A×F	2	4.57	0.0107	*
C×F×L	1	4.36	0.0373	*
A×F×L	1	4.19	0.0411	*

Statistical significance is denoted by: * ($P < 0.05$); ** ($P < 0.01$); *** ($P < 0.001$). For clarity, only the statistically significant ($P = 0.05$) main effects and interactions are presented. The error term for the degrees of freedom in all cases is 603.

high light. In 63% of the treatments, the percentage of thalli with a mass increase was lower for cut than intact lichen, occurring in 75% of the treatments at low light and 50% at low light. CA+F- was the treatment with the lowest number of mass increases for all species, and the highest for cut lichens was CA+F+. Only lichen thalli that increased in mass during the experimental period were used in the calculations of RGR.

The RGRs of damaged and intact thalli under different light and watering conditions are shown in Fig. 1, and the statistically significant results are given in Table 3. There was no effect of light level on its own, but all of the other parameters (species, cutting, quantity of water, and frequency of watering) were significant as main effects and as interactions. Frequency of watering had the greatest single effect ($F = 166.97$, d.f. = 1, 603, $P < 0.001$).

Lichen thalli of different species varied in RGR ($F = 26.10$, d.f. = 2, 603, $P < 0.001$) but the general response to the parameters was the same: cutting decreased RGR ($F = 28.78$, d.f. = 1, 603, $P < 0.001$), especially for *C. delisei* and

Table 4. Summary statistics of multivariate analysis of variance of lichen relative growth rate in the three fruticose lichens tested separately. The parameters tested: C = cut, L = light level, A = quantity of water, and F = frequency of watering.

Treatment	<i>Cetraria delisei</i>			<i>Cetraria islandica</i>			<i>Cetraria nivalis</i>		
	F	P	Sig	F	P	Sig	F	P	Sig
C	18.83	<0.0000	***				22.06	<0.0000	***
A				11.47	0.0008	***	57.30	<0.0000	***
F	93.07	<0.0000	***	54.98	<0.0000	***	35.10	<0.0000	***
C×A							14.34	0.0002	***
C×F							5.40	0.0215	*
C×L	4.77	0.0299	*						
A×F	26.60	<0.0000	***	12.02	0.0006	***			
A×L	6.47	0.0116	*				5.25	0.0233	*
F×L	12.34	0.0005	***	28.03	<0.0000	***	22.83	<0.0000	***
C×F×L				7.41	0.0070	**			
A×F×L				4.81	0.0293	*			

Statistical significance is denoted by: * ($P < 0.05$); ** ($P < 0.01$); *** ($P < 0.001$). For clarity, only the statistically significant ($P = 0.05$) main effects and interactions are presented. Degrees of freedom were 1, 239 (factor, error) for *Cetraria delisei*; 1, 215 for *Cetraria islandica* and 1, 150 for *Cetraria nivalis*.

C. nivalis, whereas a higher frequency of watering significantly increased RGR. There was a strong water quantity × frequency interaction for all species ($F = 35.06$, d.f. = 1,603, $P < 0.001$). At high frequency (F+), all species had a greater RGR with the larger quantity of water (A+). However, at the low frequency (F-), the species responded differently; *Cetraria nivalis* showed a positive response with increased quantity of water, *C. islandica* showed no effect of quantity, and *C. delisei* responded negatively. Analysis of each species separately (Table 4) revealed that there was a significant effect of quantity of water on the RGR of *C. islandica* and *C. nivalis*.

Experiment 2

The RGRs of thalli that received high quantities of water twice daily are shown in Fig. 2, together with the RGRs of lichens grown at high light intensity in experiment 1, for illustrative purposes. (There were no specific growth stages experienced by these thalli, and the growth rates in both experiments were expressed in the same units.) However, as the two experiments were run for different lengths of time, comparisons between the

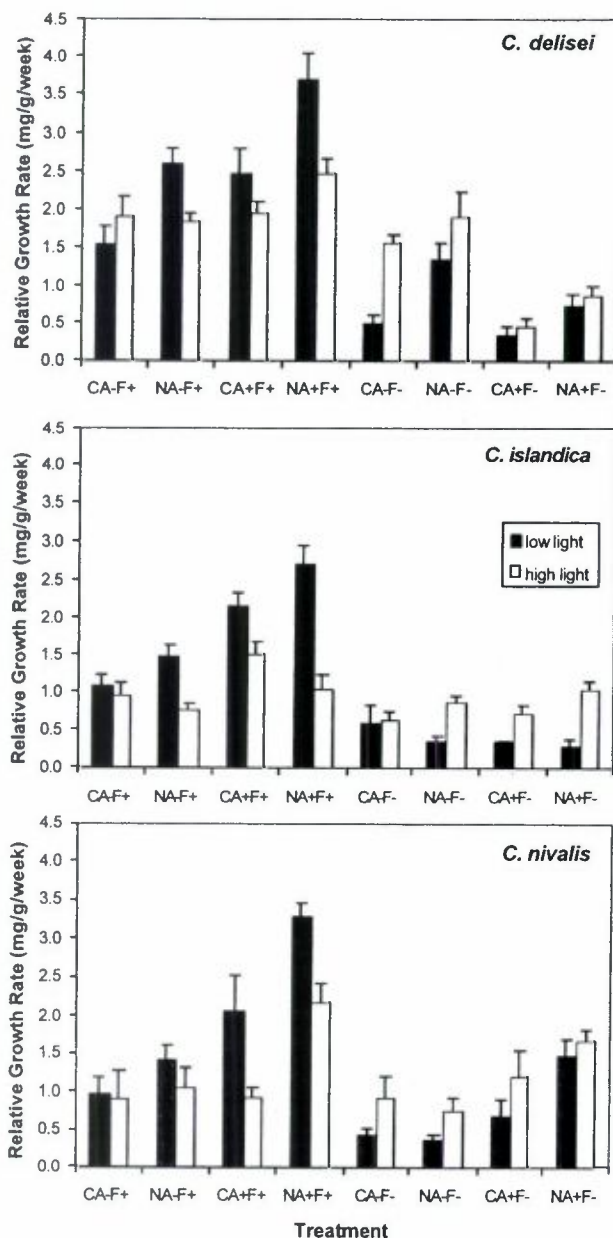


Figure 1. Relative growth rate (mg.g^{-1} per week) of damaged and intact thalli of *Cetraria delisei*, *C. islandica* and *C. nivalis* under different treatments: C = cut; N = intact; A = average daily quantity of water given (A- = 1 mm, A+ = 1.5 mm), F = weekly watering frequency (F- = 1, F+ = 3). These were carried out in 'low light', $90 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ and 'high light', $300\text{--}450 \mu\text{mol.m}^{-2}.\text{s}^{-1}$. Bars show the mean growth rate of thalli, with standard error bars. The dark bars represent the relative growth rates of lichens grown under low light levels, the light bars show the growth rate at high light levels.

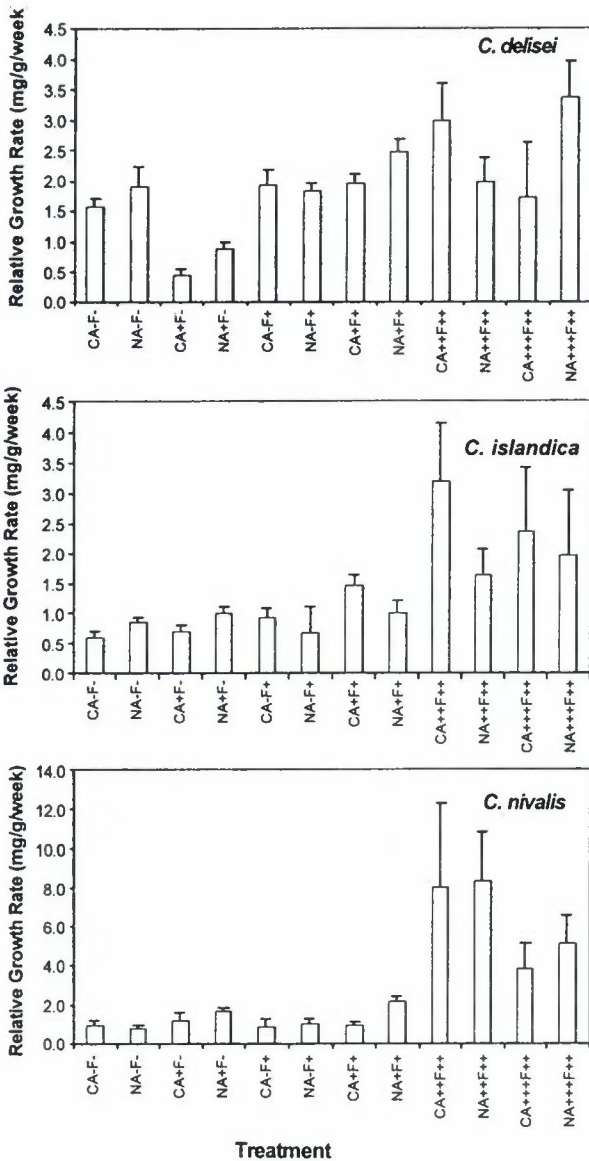


Figure 2. Relative growth rate ($\text{mg}\cdot\text{g}^{-1}$ per week) of damaged and intact thalli of *Cetraria delisei*, *C. islandica* and *C. nivalis*, grown at high light, $300\text{--}450\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and a variety of watering regimes. The RGR from both experiment 1 (12 weeks) and experiment 2 (4 weeks) are compared here. C = cut; N = intact; A = average daily quantity of water given (A- = 1 mm, A+ = 1.5 mm, A++ = 3 mm, A+++ = 5 mm), F = weekly watering frequency (F- = 1, F+ = 3, F++ = 14). The RGR are arranged in ascending order of frequency and quantity of water. Note the different scale of the y axis for *C. nivalis*.

Table 5. Amelioration effects of the treatment on cut lichens. At a particular frequency (F) of watering, the RGR of cut lichen thalli given the higher quantity (A) of water, is compared to those of intact thalli given the lower quantity. This was carried out at both light regimes individually, and using pooled data. Where there is a significant difference between the two RGR values being compared, C or N represents which of the two (cut or intact, respectively) is greatest. The RGR from both experiment 1 (12 weeks) and experiment 2 (4 weeks) are compared here.

Comparison	Species	Light	t	df	P	Sig	C vs N
Low F effect of A NA-F-/CA+F-	<i>C. delisei</i>	low	1.496	19	0.1509	ns	
		high	3.729	25	0.0009	***	N
		both	3.712	46	0.0006	***	N
	<i>C. islandica</i>	low	0.032	11	0.9753	ns	
		high	1.159	27	0.2565	ns	
		both	0.396	40	0.6945	ns	
	<i>C. nivalis</i>	low	1.467	13	0.1663	ns	
		high	1.164	17	0.2606	ns	
		both	1.629	32	0.1132	ns	
High F effect of A NA-F+ /CA+F+	<i>C. delisei</i>	low	0.339	40	0.7367	ns	
		high	0.638	30	0.5281	ns	
		both	0.076	72	0.9398	ns	
	<i>C. islandica</i>	low	2.885	40	0.0063	**	C
		high	3.575	28	0.0013	**	C
		both	3.907	70	0.0002	***	C
	<i>C. nivalis</i>	low	2.386	29	0.0238	*	C
		high	0.435	17	0.6687	ns	
		both	1.582	48	0.1203	ns	
V. high F effect of A NA++F++ /CA+++F++	<i>C. delisei</i>	high	0.329	14	0.7472	ns	
	<i>C. islandica</i>	high	0.512	23	0.6135	ns	
	<i>C. nivalis</i>	high	1.653	8	0.1370	ns	
Low A effect of F NA-F-/CA-F+	<i>C. delisei</i>	low	0.300	36	0.7655	ns	
		high	0.024	28	0.9812	ns	
		both	0.165	66	0.8696	ns	
	<i>C. islandica</i>	low	3.720	29	0.0008	***	C
		high	0.420	25	0.6777	ns	
		both	2.827	56	0.0065	*	C
	<i>C. nivalis</i>	low	2.227	16	0.0407	*	C
		high	0.392	13	0.7018	ns	
		both	1.683	31	0.1024	ns	
High A effect of F NA+F-/CA+F+	<i>C. delisei</i>	low	4.009	30	0.0004	***	C
		high	5.629	29	< 0.0000	***	C
		both	6.158	61	< 0.0000	***	C
	<i>C. islandica</i>	low	6.946	31	< 0.0000	***	C
		high	2.309	29	0.0283	*	C
		both	6.237	62	< 0.0000	***	C

Table 5. Continued

Comparison	Species	Light	t	df	P	Sig	C vs N	
Increased F and A NA+F+ /CA++F++	<i>C. nivalis</i>	low	2.077	28	0.0471	*	C	
		high	3.455	16	0.0033	**	N	
		both	0.389	46	0.6994	ns		
	<i>C. delisei</i>	high	0.973	25	0.3397	ns		
		<i>C. islandica</i>	high	1.296	26	0.2063	ns	
			<i>C. nivalis</i>	high	2.797	11	0.0174	*

RGRs should be made with caution. Validity of comparison was possibly affected by predrying the thalli and thus the proportion of the growth potentially respired in the air-drying stage, and so the real growth rates measured in the shorter experiment may have been underestimated. The RGRs were generally higher with F++ than with F+. The degree of the response varied between species, with *C. islandica* and *C. nivalis*, in particular, responding greatly to the increased watering and frequency treatments. All species responded to quantity and frequency of water addition with significantly higher growth at A+++F++ compared to A+F+ (F value = 10.28, d.f. = 1,132, $P < 0.01$). *C. nivalis* had significantly higher growth rates both at A++F++ (F value = 23.54, d.f. = 1, 23, $P < 0.001$), and at A+++F++ (F value = 8.40, d.f. = 1, 31, $P < 0.01$) than at A+F+.

There was no significant effect of the cutting treatment or the quantity of water when watered twice daily for any of the species in experiment 2. This suggests that the frequency of watering was the most important parameter for the growth of the lichens, and increased frequency of watering thus ameliorated the negative effect of cutting thalli.

Amelioration effect of increased watering

The RGRs of intact thalli at a set frequency of watering were compared (using t-tests) to those of cut thalli receiving an increased quantity of water. Likewise, while keeping the quantity of water the same, intact thalli RGR were compared to those of cut thalli that received a higher frequency of watering. These results are shown in Table 5. The comparisons were carried out at high and low light levels separately, and also using pooled light data. In most cases, the RGRs of cut thalli receiving more water or more frequent

watering were not significantly different from, or were even higher than, those of intact thalli in the lower watering regime. Thus, for most species and treatments investigated here, the addition of more water, or more frequent watering more than compensated for the reduction in growth rates due to the cutting of the thalli. The cases where this did not occur were both at high light: *C. delisei* at F- had a lower RGR with more water, and *C. nivalis* at A+ had a higher RGR when it received its water all at once rather than three times during the week.

4. Discussion

Species differences

Species differences in RGR may be partly related to morphological differences, especially in their ability to capture and hold water (Sundberg, 1999). Thalli of *Cetraria nivalis* are relatively flat compared to the other species studied, and were observed not to hold surface films of water as effectively as *C. islandica* or the very highly branched *C. delisei*, thereby allowing water to run off quickly. *C. delisei*, which had the highest RGR, had the highest surface area to mass ratio as it was far more branched than the other species studied. A greater water holding capacity prolongs the photosynthetic period leading to an increase in RGR. This interspecies difference is particularly apparent if the RGR given the lowest water quantity A- are compared across species, especially at F-. At very high watering frequency (F++) used in experiment 2, *C. nivalis* had the highest RGR at both A++ and A+++.
C. nivalis needs higher irradiance for light compensation and saturation of photosynthesis than *C. delisei* (Schipperges, 1992), and this, coupled with non-limiting water availability promotes higher growth rates.

Effect of cutting

Armstrong (1973) worked on the radial growth of *Parmelia* thalli and recorded that a few fragmented thalli had a lower growth rate than a non-fragmented thallus of the same size. However, he found that the variability in RGR of thalli of equal size exposed to similar conditions was so high (Armstrong, 1974a) that he could not find conclusive evidence that the radial growth slowed after fragmentation (Armstrong, 1974b). We have shown that cutting fruticose lichen thalli into small pieces reduced both their ability to gain mass and their growth rate, during a three-month growing period. We recorded a growth rate of cut thalli that was 15 to 63% lower (depending on species and treatment) than comparative intact thalli. Longer-term

experiments would be useful to indicate whether any recovery could be expected in the growth rate of cut lichens (Armstrong, 1979) some time after the damage was done. In a field experiment using *Cladonia mitis*, Gaare (1986) demonstrated that even after six years, clipped thalli had 7% lower growth than untreated controls. Therefore serious long-term damage can be caused to lichen fields by reindeer trampling and by groups of people walking during the summer when the thalli are dry, brittle and most susceptible. The reduced growth rate of damaged thalli contributes to the slow recovery which may take 20 years or more (Hale, 1974).

Effect of watering frequency

Mean daily rainfall has been shown to be the controlling factor of RGR of lichens in the field in mainland Scandinavia and Wales (Kärenlampi, 1971; Armstrong, 1993). The authors are not aware of previous studies separating the effects of frequency and quantity of rainfall. Frequency of watering is an important factor influencing the RGR, since lichens can photosynthesise only when wet. By increasing the frequency of wetting, the lichens had an increased time to gain carbon. We have shown that the frequency of watering was the treatment with the greatest effects on growth rate. Both increased frequency of water addition and increased quantity of water ameliorated the damage done to cut lichens, enabling the RGR to reach or exceed that of intact thalli under a normal regime.

Global climate models predict increases in temperature and precipitation in northern latitudes, but at present they are not sufficiently refined to be able to predict the distribution of the projected rainfall patterns (IPCC, 1995, J.G. Winther, pers. com.). However, changing rainfall patterns will be a key factor in determining the future growth of lichens. The interaction between frequency and quantity of rainfall is important in the determination of the response of lichen growth to increased precipitation. Totally different responses of lichen growth would be expected from sporadic, heavy rain showers, than from more evenly distributed rainfall or drizzle. Temperature increases will result in a higher proportion of the precipitation falling as rain, rather than snow, a phenomenon already recorded (Førland and Hanssen-Bauer, 2000).

Effect of water quantity

The quantity of water given to the lichens affected RGR; this response was frequency and species dependent. When frequency was high (F+), all three species could make use of a greater quantity of water and respond with higher RGR, whereas at low frequency (F-) (experiment 1) and very high frequency

(F++) (experiment 2), increasing the quantity of water given (A+ and A+++, respectively) did not increase RGR. Excess water may potentially limit the photosynthetic activity of the lichen, swelling the fungal hyphae and thus impeding the diffusion of CO₂ to the photobiont (Kappen and Breuer, 1991; Palmquist, 1995). *C. delisei*, possibly morphologically adapted to retain water more effectively, was thus swamped when it received a high quantity of water (A+), at low frequency (F-), and therefore responded negatively.

Effect of light level

Light did not appear to limit growth since there was no significant effect of light intensity on RGR. These results suggest that lower light levels resulting from increased cloud cover would not inhibit lichen growth. It may be that both the light compensation and saturation points of the lichens used were low, i.e. under 90 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$, or that there was acclimation to low light levels. Lichens are generally adapted to low light environments and therefore exhibit a saturating response at 100-400 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ (Demmig-Adams et al., 1990). The highest light intensities experienced here are not likely to be high enough to induce photoinhibition of net photosynthesis, as found by Coxson (1987) nor to cause a decrease in photochemical efficiency (Demmig-Adams et al., 1990). Published values of light compensation points for most Arctic and alpine species of vascular plants are in the range of 25-92 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ at 20°C (Mooney and Johnson, 1965; Scott and Menalda, 1970; Tieszen, 1973). The light compensation point of photosynthesis decreases with decreasing temperature for Arctic vascular plants (Scott and Billings, 1964) and alpine herbs (Rawat and Purohit, 1991). Regehr and Bazazz (1976) reported a shift in light compensation point from 75 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ at 25°C to 18 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ at 5°C. We could therefore expect the light compensation point to be under 90 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ for these lichens grown at 6°C. Light penetration through a 3.5 cm snow cover constitutes only 10% of light in the photosynthetically active wavelengths (Kimball et al., 1973), and so a low light compensation point may act as an adaptation to low light intensity under shallow layers of snow.

At the low light level, there was a strong reduction in the number of thalli that gained mass during the experiment, especially at low watering frequency, and particularly for cut thalli. Lechowicz (1981) found that lichen biomass decreased when the thalli were only wet for a short time, corresponding to the infrequent watering treatment, F-. It is likely therefore, that the lichens lost mass when their carbon balance was negatively affected, for example by high resaturation respiration occurring (Smith and Molesworth, 1973; Farrar and Smith, 1976) when there was relatively low photosynthetic activity.

Comparison of laboratory and field data

Whole lichen thalli have not been grown successfully in artificial environments (Armstrong, 1979; Sundberg, 1999) prior to this study, and there have been few field studies of RGR of fruticose lichens in the High Arctic with which to compare our data. However, our growth rates for intact thalli are within the same range, for similar rainfall, as those measured in various parts of Scandinavia by Kärenlampi (1971), Gaare (1986), Crittenden et al. (1994) and Sundberg (1999). The annual dry mass accumulation for a variety of fruticose and foliose lichen species worldwide is reported to be between 4 and 40% (Denison, 1988; Boucher and Nash, 1990; Sillet, 1994; McCune et al., 1996; Renhorn, 1997). The growth rates of *Cetraria* species under the conditions we investigated were at the lower end of this spectrum.

The RGR of intact thalli at the lower light level presented in this paper were slightly lower than, but of the same order of magnitude as those measured by Cooper and Wookey (2001) in the field in 1999. Laboratory RGR were: *Cetraria delisei* 3.7 ± 0.3 , *C. islandica* 2.6 ± 0.2 , *C. nivalis* 3.3 ± 0.2 mg.g⁻¹ per week compared to field rates of 6.0 ± 0.9 , 6.0 ± 1.3 , 6.0 ± 0.8 mg.g⁻¹ per week, respectively. The small differences between the laboratory and field rates may be partly due to differences in light quality, humidity, temperature, or methodology. However, the main cause is probably the higher rainfall experienced by the lichens in 1999 than in the experiment. Summer 1999 was wetter than normal: the average daily rainfall in the period June 16 – September 15 was higher in 1999 than the previous 10 years (1.28 mm compared to 1.08 mm) and the average amount for each rainfall event was 24% higher in 1999. Precipitation in 1999 was recorded approximately three times a week during this period (data from the Norwegian Meteorological Office). In addition, a recent paper (Førland and Hanssen-Bauer, 2000) suggests that precipitation measurement in Svalbard has underestimated rain and snowfall; the true values for the annual precipitation at Ny Ålesund are speculated to be about 50% higher than the measured quantity. If this is so, then it has a serious implication for the interpretation of the absolute values of our experiments here. Thus, the treatment A+F+ is possibly closer to the actual average quantity and frequency of precipitation received by the lichens studied in Svalbard in 1999.

Environmental manipulations to simulate possible future climatic conditions have been carried out at the community level, throughout the circumpolar Arctic and Subarctic (Arft et al., 1999). Experimental warming and increased nutrient availability in Subarctic areas showed a reduction in lichen cover (Cornelissen et al., in press). This suggests that lichens may become excluded though light and water competition by taller and faster growing vascular

plants, leading to a possible long-term reduction in lichen growth in the Subarctic. A decline in lichen cover was not found in the High Arctic sites; lichen growth at the extreme latitudes may be controlled to a greater extent by climatic rather than biotic factors. In water-limited areas of the High Arctic, it is possible that taller vascular plants could intercept rainwater, and their architecture could thus alter the local spatial distribution of water, to the disadvantage of lichens. However, competitive interactions in the High Arctic are very different from the Subarctic (Callaghan et al., 1991) and so responses recorded in the Subarctic should be interpreted with caution when trying to predict the response in the High Arctic.

5. Conclusion

To our knowledge, this is the first laboratory study of the growth rates of High Arctic forage lichen thalli in a controlled environment. Lichen thalli that were cut into small pieces grow at slower rates than intact thalli, but show that there is potential for these small fragments to recolonise the previous lichen-rich areas of Brøggerhalvøya which were trampled and grazed by reindeer. A higher frequency of rainfall events and a greater volume of rain, as predicted by climate change models, could increase the growth rates of these fragments and help to ameliorate the damage done to the lichens by reindeer. These data should be evaluated in conjunction with other studies to estimate the relative contribution of the effects of competition by plants for light and water, and damage by animals through grazing and trampling, before long term estimates of changes in lichen biomass can be made.

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REFERENCES

- Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R.D., Jónsdóttir, I.S., Laine, K.,

- Lévesque, E., Marion, G.M., Molau, U., Mølgaard, P., Nordenhäll, U., Raszhivin, V., Robinson, C.H., Starr, G., Stenström, A., Stenström, M., Totland, Ø., Turner, P.L., Walker, L.J., Webber, P.J., Welker, J.M., and Wookey, P.A. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. *Ecological Monographs* **69**: 491–511.
- Armstrong, R.A. 1973. Seasonal growth and growth rate-colony size relationships in six species of saxicolous lichens. *New Phytologist* **72**: 1023–1030.
- Armstrong, R.A. 1974a. The structure and dynamics of saxicolous lichen communities. D.Phil. Thesis, University of Oxford.
- Armstrong, R.A. 1974b. Growth phases in the life of a lichen thallus. *New Phytologist* **73**: 913–918.
- Armstrong, R.A. 1979. Growth and regeneration of lichen thalli with the central portions artificially removed. *Environmental and Experimental Botany* **19**: 175–178.
- Armstrong, R.A. 1993. Factors determining lobe growth in foliose lichen thalli. *New Phytologist* **124**: 675–679.
- Bayfield, N.G., Urquhart, U.H., and Cooper, S.M. 1981. Susceptibility of four species of *Cladonia* to disturbance by trampling in the Cairngorm mountains, Scotland. *Journal of Applied Ecology* **18**: 303–310.
- Beadle, C.L. 1985. Plant growth analysis. In: *Techniques in Bioproductivity and Photosynthesis*. J. Coombs, D.O. Hall, S.P. Long, and J.M.O. Scurlock, eds. Pergamon Press Ltd., Oxford, pp. 20–39.
- Boucher, V.L. and Nash, T.H. III. 1990. Growth patterns in *Ramalina menziesii* in California: coastal vs. inland population. *Bryologist* **93**: 295–309.
- Brattbakk, I. 1986. Flora og vegetasjon. In: *Svalbardreinen og dens livsgrunnlag*. N.A. Øritsland, ed. Universitetsforlaget, Oslo, pp. 15–34.
- Callaghan, T.V., Press, M.C., Lee, J.A., Robinson, D.L., and Anderson, C.W. 1991. Spatial and temporal variability in the responses of Arctic terrestrial ecosystems to environmental change. *Polar Research* **18**: 191–197.
- Cooper, E.J. 1996. An ecophysiological investigation of some species of Arctic and temperate *Ranunculus* L. with respect to climate warming. Ph.D. Thesis. University of Bradford, 267 pp.
- Cooper, E.J. and Wookey, P.A. 2001. Field measurements of the growth rates of forage lichens, and the implications of grazing by Svalbard reindeer. *Symbiosis* **31**: 173–186.
- Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E., Hik, D.S., Hobbie, S.E., Press, M.C., Robinson, C.H., Henry, G.H.R., Shaver, G.R., Phoenix, G.K., Gwynn Jones, D., Jonasson, S., Chapin, III F.S., Molau, U., Neill, C., Lee, J.A., Melillo, J.M., Sveinbjörnsson, B., and Aerts, R. Global change may cause lichen decline in Arctic ecosystems through increases in vascular plant biomass. *Journal of Ecology*, in press.
- Coxson, D. 1987. Photoinhibition of net photosynthesis in *Stereocaulon virgatum* and *S. tomentosum*, a tropical-temperate comparison. *Canadian Journal of Botany* **65**: 1707–1715.
- Crittenden, P.D., Kalucka, I., and Oliver, E. 1994. Does nitrogen supply limit the growth of lichens? *Cryptogamic Botany* **4**: 143–155.
- Demmig-Adams, B., Maguas, C., Adams, W.W. III, Meyer, A., Kilian, E., and Lange, O.L. 1990. Effect of high light on the efficiency of photochemical energy conversion in a

- variety of lichen species with green and blue-green phycobionts. *Planta* **180**: 400–409.
- Denison, W.C. 1988. Culturing the lichens *Lobaria oregana* and *L. pulmonaria* on nylon monofilament. *Mycologia* **80**: 811–814.
- Ditlefsen, A.M. 2000. *Reinbeite på Brøggerhalvøya, Svalbard – en oppfølgende beiteøkologisk undersøkelse III*. Hovedoppgave ved Institutt for biologi og naturforvaltning, Norges Landbruks Høgskole, Ås. 57 pp.
- Farrar, J.F. and Smith, D.C. 1976. Ecological physiology of the lichen *Hypogymnia physodes*. III. The importance of the rewetting phase. *New Phytologist* **77**: 115–125.
- Førland, E.J. and Hanssen-Bauer, I. 2000. Increased precipitation in the Norwegian Arctic: true or false? *Climatic Change* **46**: 485–509.
- Gaare, E., 1986. Does grazing influence growth of the reindeer lichen *Cladina mitis*? *Rangifer* **1**: 357–358.
- Hale, M.E. 1974. *The Biology of Lichens*. Edward Arnold, London, 181 pp.
- IPCC Second Assessment Report: Climate Change. 1995. *A Report of the Intergovernmental Panel on Climate Change*. IPCC, Geneva, Switzerland, 64 pp.
- Jónsdóttir, I.S., Crittenden, P.D., and Fagerbrand, A. 1999. Measuring growth rate in bryophytes and lichens. In: *Plant Response to Climate Change: Integration of ITEX Discoveries*. R.D. Hollister, ed. Proceedings from the 9th ITEX Meeting, January 5–9, 1999. pp. 91–95.
- Kappen, L. and Breuer, M. 1991. Ecological and physiological investigations in continental Antarctic cryptogams. II. Moisture relations and photosynthesis of lichens near Casey Station, Wilkes Land. *Antarctic Science* **3**: 273–278.
- Kattenberg, A., Gruza, G.V., Jouzel, J., Karl, T.R., Ogallo, L.A., and Parker, D.E. 1996. Observed climate variability and change. In: *Climate Change 1995 – The Science of Climate Change*. J.T. Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, Kattenberg, A., and K. Maskell, eds. Cambridge University Press, Cambridge, UK, pp. 289–357.
- Kimball, S.L., Bennett, B.D., and Salisbury, F.B. 1973. The growth and development of montane species at near-freezing temperatures. *Ecology* **54**: 168–173.
- Kärenlampi, L. 1971. Studies on the relative growth rate of some fruticose lichens. *Reports from the Kevo Subarctic Research Station* **7**: 33–39.
- Lechowicz, M.J. 1981. The effects of climatic pattern on lichen productivity: *Cetraria cucullata* (BELL) ACH., in the Arctic tundra of Northern Alaska. *Oecologia* **50**: 210–216.
- McCune, B., Derr, C.C., Muir, P.S., Shirazi, A., Sillet, S.C., and Daly, W.J. 1996. Lichen pendants for transplantation and growth experiments. *Lichenologist* **28**: 161–169.
- Mooney, H.A. and Johnson, A.W. 1965. Comparative physiological ecology of an Arctic and alpine population of *Thalictrum alpinum*. *Ecology* **46**: 721–727.
- Palmquist, K. 1995. Uptake and fixation of CO₂ in lichen photobionts. *Symbiosis* **18**: 95–109.
- Rawat, A.S. and Purohit, A.N. 1991. CO₂ and water vapour exchange in four alpine herbs at two altitudes and under varying light and temperature conditions. *Photosynthesis Research* **28**: 99–108.
- Regehr, D.L. and Bazzaz, F.A. 1976. Low temperature photosynthesis in successional winter annuals. *Ecology* **57**: 1297–1303.
- Renhorn, K.E. 1997. Effect of forestry on biomass and growth of epiphytic macrolichens in boreal forests. Ph.D. Thesis. Umeå University, Sweden.

- Schipperges, B. 1992. Patterns of CO₂ gas-exchange and thallus water content in Arctic lichens along a ridge profile near Ny Ålesund, Svalbard. *Polar Research* 11: 47-68.
- Scott, D. and Billings W.D. 1964. Effects of environmental factors on standing crop and productivity of an alpine tundra. *Ecological Monographs* 34: 243-270.
- Scott, D. and Menalda, P.H. 1970. Carbon dioxide exchange of plants. II. Response of six species to temperature and light intensity. *New Zealand Journal of Botany* 8: 361-368.
- Sillet, S.C. 1994. Growth rates of two epiphytic cyanolichens at the edge and in the interior of a 700-year old Douglas fir forest in the western Cascades of Oregon. *Bryologist* 97: 321-324.
- Smith, D.C. and Molesworth, S. 1973. Lichen physiology. XIII. Effects of rewetting dry lichens. *New Phytologist* 72: 525-533.
- Sundberg, B. 1999. Physiological ecology of lichen growth. Ph.D. Thesis, Umeå University, 119 pp.
- Thomson, J.W. 1984. *American Arctic Lichens. 1. The Macrolichens*. Columbia University Press, New York.
- Tieszen, L.L. 1973. Photosynthesis and respiration in Arctic tundra grasses: field light intensity and temperature responses. *Arctic and Alpine Research* 5: 239-251.