

GROWTH RATES OF *Cladonia rangiferina* (L.) Web. ON SOUTH GEORGIA

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ABSTRACT. Mean net production of *C. rangiferina* on South Georgia after 100 days is up to 127.3 g./m.² and the mean annual linear growth rate is calculated to be up to 5.33 mm./yr. but both decline with increasing altitude. Studies on the regeneration of *C. rangiferina* indicate that, although it has the potential to restore lichen swards in areas heavily grazed by reindeer, the density of reindeer is too high for this to occur.

SPECIES of *Cladonia* are often of considerable ecological importance in a number of plant communities on the sub-Antarctic island of South Georgia (lat. 54°S., long. 37°W.), particularly as they appear to form part of the diet of the island's introduced reindeer. Preliminary studies on the growth rate of the most abundant species, *C. rangiferina* (L.) Web., were made during the 1971-72 austral summer first to provide a comparison with the same species in Arctic regions, where it and related species ("reindeer lichens") are economically important as reindeer fodder, and secondly to provide data in conjunction with studies on the influence of reindeer grazing on South Georgian plant communities with particular reference to lichens. From this investigation, estimates of the time required for recovery of overgrazed areas on the island may be made.

DRY-WEIGHT INCREASE AND NET PRODUCTION OF PODETIA

Method

The method employed was a modification and simplification of that used in Finland by Kärenlampi (1971). *Cladonia rangiferina* was collected from lichen-rich *Festuca erecta* (= *F. contracta*) grassland at 30 m. a.s.l. below Gull Lake, Cumberland East Bay, by removing several large (c. 400 cm.²) dense colonies, including the decaying bases of podetia, and transporting them to the laboratory on large trays. Containers were made similar to those of Kärenlampi (1971), but were short Perspex cylinders 10 cm. in diameter by 5 cm. deep with a fine wire mesh glued across one end to allow throughfall of precipitation. Material from the colonies, with dead and decaying blackish parts of podetia removed, was placed in each container as far as possible at the same density as the original sward. A total of 36 containers was prepared. Each container, of known weight, was then left with its lichen sample in the laboratory at c. 18° C until a constant air-dry weight had been reached. 18 replicates were then transferred to each of two sites, at 30 m. a.s.l. and 150 m. a.s.l., on the south-facing slopes of Mount Duse, Cumberland East Bay. In order to give some protection from strong winds which may have removed podetia from the containers, each site was in a depression in more or less level ground.

The containers were placed in position at each site on 28 November 1971 and the experiment terminated on 8 March 1972, thus giving an overall growing period of 100 days. It was not possible to re-weigh the samples more frequently owing to the author's frequent absences from the Cumberland Bay area. After a period of air drying to constant weight, it was confirmed that the weights of the containers were unchanged and that increase in dry weight was due solely to that of the podetia.

The water content of air-dry podetia was estimated in a manner similar to that of Kärenlampi (1971), whereby the air-dry weights of 50 additional samples of *C. rangiferina* were determined. The samples were then oven-dried at 110° C to constant weight. The mean weight loss of the 50 samples was 24.5 per cent of the air-dry weight, with a standard deviation of 2.36. This figure was then used to compute the increase in net dry weight.

Results

The dry-weight and net-production data for podetia growing at the two sites for 100 days are summarized in Table I. Although the mean dry weight increases were small, 1.00 g. and 0.77 g. for the low- and high-altitude sites, respectively, they reflect a slight reduction in growth at the

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TABLE I. DRY-WEIGHT INCREASE AND NET PRODUCTION IN 10 cm. BY 5 cm. CORES OF *Cladonia rangiferina* AT TWO SITES AFTER 100 DAY GROWING PERIOD

Site altitude (m.)	Mean dry weight/core (g.)		Mean increase in dry weight/core (per cent, with standard deviation)	Mean net production (g./m. ²)
	Day 0	Day 100		
30	16.08	17.08	6.2 ± 1.70	127.3
150	15.58	16.35	4.9 ± 1.66	98.0

higher, more exposed site. This difference is not, however, statistically significant. Mean net dry-weight production values for the growing period are relatively high, particularly at the lower site. The test period, from late November to early March, was during the most favourable part of the summer. The growing season, however, may commence as early as late October, when the winter snow cover melts, and continues until early April. Although the test period undoubtedly covered the weeks of maximum growth, it is likely that some growth had already occurred prior to the start of the experiment and would have continued after its termination. Thus it is not valid to extrapolate from the data to produce values for the whole growing season.

Detached litter, consisting of small fragments of podetia broken off by wind or rough handling totalled 0.44 g. for the 18 low-altitude containers, but none was found at the high-altitude site. This may have been due to the more exposed position of the latter, so that any litter may have been blown away.

INCREASE IN LENGTH OF PODETIA

Method

The linear growth of podetia was measured using the formula given by Andreev (1954):

$$\frac{\text{Height of living part of podetium}}{\text{Number of nodes on living part of podetium}} = \text{Mean annual growth rate of podetium.}$$

The living part of the podetium is easily distinguished from the dead basal part by the difference in colour and texture between the two.

Samples of 50 podetia were collected from colonies of *C. rangiferina* growing at 30 m. a.s.l. near Gull Lake and at 150 m. a.s.l. on the northern slopes of Brown Mountain nearby, and subjected to a morphological analysis. Unlike the work of Kärenlampi (1970, 1971), this analysis was not intended to investigate in detail the growth of various parts of the podetium but to indicate whether altitude, and consequently variation in temperature and exposure, has any significant effect on growth rate, so that a better interpretation of the previous experiment may be attempted.

The mean length and mean number of nodes were determined for each sample and from this the mean age of the podetia was calculated. In addition, a number of internodes were measured to investigate the length of time during which elongation occurred at each internode. Because of difficulty in measuring the very short internodes at the tips of the podetia, measurements commenced at node 2 below the apex, the internode between this and node 3 being called internode 3, etc. Measurement of internode length was not possible beyond internode 7, where the complexity of branches of some podetia prevented accurate measurement. All measurements were made on moist samples, since podetia shrink and become brittle when dry.

Results

The variation in internode length of the 50 podetia from the low- and high-altitude sites is summarized in Table II. Mean annual growth was greater at 30 m. (5.33 mm./yr.) than at 150 m. (4.65 mm./yr.), the difference being statistically significant. Since there is virtually no difference in the number of nodes on podetia from the two sites, the difference in mean annual linear growth must be due to variation in length of internode. For internodes 3-5 there was no significant difference between the lengths, although the internodes of the podetia from the

TABLE II. MEAN INTERNODE LENGTH OF 50 *Cladonia rangiferina* PODETIA FROM TWO SITES

Site	Mean number of nodes	Mean total length of living podetium (mm.)	Mean length of internode (mm.)					Mean annual linear growth (mm.)
			3	4	5	6	7	
Low altitude (30 m.)	12.3 ± 1.3	65.6 ± 2.5	3.14 ± 0.90	4.50 ± 1.22	5.35 ± 1.20	5.69 ± 1.16	6.36 ± 1.24	5.33 ± 0.80
High altitude (150 m.)	12.4 ± 1.3	57.5 ± 3.0	3.55 ± 1.22	5.06 ± 1.09	5.29 ± 1.37	6.28 ± 1.19	5.30 ± 0.71	4.65 ± 0.90
Significance of difference	NS	*	NS	NS	NS	*	**	*

NS Not significant. * Significant at 5 per cent level. ** Significant at 1 per cent level.

high-altitude site tended to be slightly longer. However, the intersite differences in length for internodes 6 and 7 were statistically significant. It is thus possible that internode elongation occurs beyond internode 7 on low-altitude plants, but ceases at that point in plants grown at higher altitudes. Measurements of internodes 8 onwards would have provided data which may have solved this, but the complexity of branching at that level on the podetia prevented this.

DISCUSSION

Although *Cladonia rangiferina* and related species ("reindeer lichens") are of considerable ecological importance as reindeer fodder in boreal forest and tundra vegetation, there are comparatively few data regarding their rates of growth and production. South Georgia has a cool oceanic climate (Smith, 1971), probably more oceanic than any of the other regions from which growth rates of *C. rangiferina* have been reported (Pegau, 1968, table 2). Annual precipitation is c. 1,400 mm., c. 600 mm. of which falls during the November–March growing season. The mean annual temperature is 1.8°C , but there is a relatively small diurnal and seasonal amplitude, the mean for the coldest month (August) being -1.8°C and that for the warmest month (February) being 5.4°C . The relatively low air temperatures, especially during the summer months, may be considered to have a retardatory effect on growth rates, but the micro-environment experienced by the lichen is often much more favourable than is indicated by the ambient conditions. Since growth rates of reindeer lichens have been shown to be directly proportional to amount of rainfall (Kärenlampi, 1971), the high precipitation on South Georgia may explain why growth rates of *C. rangiferina* there are as high as those of the same species growing in more favourable summer climates in the Arctic.

Some data relating to the growth of *C. rangiferina* on South Georgia have been obtained by two methods. The first, involving increase in dry weight of the podetia, has been used by Kärenlampi (1971) to investigate relative growth rates of several lichens important as reindeer fodder. This method relates only to the living parts of podetia and so only a gross growth rate can be obtained. Since the podetia are in the "podetium-renewal phase" as shown by the presence of the decaying basal layer (Andreev, 1954; Ahti, 1959), it can be assumed that during this phase increase in dry weight of the living part of the podetium is balanced by a corresponding decrease in the dry weight of the decaying base.

Kärenlampi (1971) showed that relative growth rate was directly proportional to rainfall, other factors such as insolation and temperature having only a small influence. It was not possible to undertake micro-climatic studies at the sites on South Georgia, but a qualitative measure of exposure at the two sites would suggest lower temperatures and greater saturation deficits at the higher site. Although the data presented in Table I suggest that dry weight and net production decrease slightly with increasing altitude, this is not borne out by a statistical analysis of the data. However, many more data are required before it can be established definitely that variation in altitude has no effect on growth rate.

The second method, an estimate of mean annual linear growth, has been used more widely, but it is based on the premise that only one node is formed per podetium per year. It is possible, however, that more than one node may be produced in exceptionally favourable summers. Extra nodes may also be formed by regeneration of damaged podetia. Andreev's (1954) formula provides a useful method for the rapid comparison of the extension growth of Cladoniae in various regions. Some data for *C. rangiferina* have been summarized by Pegau (1968, table 2), which showed that the mean annual linear growth rate of this species varied from 2.7 mm./yr. in tundra communities on Chukotsk Peninsula, western Siberia, to 5.6 mm./yr. in spruce forest on Seward Peninsula, Alaska, both sites being at c. lat. 65°N . In agreement with Kärenlampi's (1971) hypothesis, Pegau considered that growth rates are proportional to amount of rainfall. The growth rate on South Georgia has been shown to be up to 5.33 mm./yr., possibly a reflection of the high precipitation on this oceanic island. Few data, however, have been published on the variation in lichen growth rates that may occur between different habitats. Lechowicz and Adams (1972) recorded the mean annual growth rate of *C. mitis* in Wisconsin as 5.2 ± 0.2 mm./yr., but they noted that growth rates did not differ between podetia growing in full sun and in shade. While insolation may have little effect on growth rate, exposure, crudely measured by altitude, does appear to have some effect. A significant difference was found

between the mean lengths of the living part of podetia of *C. rangiferina* at altitudes of 30 and 150 m. Since the sites were barely 1 km. apart, this difference could probably not be attributed to variation in precipitation but rather to the increased exposure and lower temperatures at the higher site. Thus some caution must be exercised when comparing growth rates of Cladoniae from different regions, since other factors besides rainfall may have an influence. While increase in altitude appears to depress the growth rate of the older internodes of podetia of *C. rangiferina*, it does not appear to affect internode production. Thus, while the dry-weight increase of comparable internodes at the two sites is roughly the same, increase in length in corresponding older internodes decreases at higher altitudes.

Regarding regeneration of lichen swards grazed by reindeer, Andreev (1954) has shown that the time required for complete regeneration is directly proportional to the amount of podetium grazed, from less than 5 years when up to one-third of the podetium is grazed to over 15 years when most of the podetium is grazed. Preliminary experiments conducted by the author at Birmingham on the regeneration of South Georgian *C. rangiferina* indicate that regeneration occurs rapidly in damaged podetia, even those totally fragmented, and may occur from any part of the living portion of the podetium. After 5 months, fragmented podetia growing on moist peat outdoors, during winter, had produced a number of small branches up to 1.2 mm. long and 0.6 mm. in diameter. Despite this apparently rapid regeneration, swards of Cladoniae are now totally absent in the areas of South Georgia which are grazed by reindeer (Lindsay, 1973). Regeneration of such swards has probably been prevented by the high density of reindeer on South Georgia when compared to Arctic regions. On the peninsula on the north shore of Royal Bay, the density of reindeer was estimated in 1972 to be over 14/km.² (Lindsay, 1973), a density much greater than that allowed by range management in Scandinavia (Skuncke, 1969). Despite the relatively high growth rates and apparently rapid regeneration capacity of *C. rangiferina* on South Georgia, there appears to be little chance of the recovery of lichen swards in areas grazed by reindeer while the latter continue at their present density.

ACKNOWLEDGEMENTS

I wish to thank Dr. R. I. L. Smith for valuable criticism of the manuscript. I am grateful to Professor J. G. Hawkes, Mason Professor of Botany, University of Birmingham, for facilities provided in the Department of Botany.

MS. received 15 July 1974

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