GROWTH AND PRODUCTION OF *Cladonia rangiferina* AND *Sphaerophorus globosus* ON SIGNY ISLAND, SOUTH ORKNEY ISLANDS

By T. N. Hooker*

ABSTRACT. The growth of *Cladonia rangiferina* and *Sphaerophorus globosus* was determined on Signy Island, South Orkney Islands. Mean annual production for the two lichens was 84.4 and 34.1 mg g^{-1} dry weight, respectively, over a period of 119 d spanning most of the growing season. There was no correlation between growth rate and altitude above sea-level (15–100 m). The main growth period was recorded in the summer and autumn months with little, if any, growth occurring during the spring months. Photographs of *S. globosus* demonstrated a rate of linear increase of podetia of approximately 2 mm $year^{-1}$ in mature colonies. Podetia in a juvenile colony (6 mm diameter) grew approximately 0.5–0.8 mm $year^{-1}$.

MOST growth studies of fruticose lichens have been applied to *Cladonia rangiferina* and related species. These lichens are of considerable ecological and economic importance as reindeer fodder in boreal forest and tundra vegetation where knowledge of growth rates is essential for efficient range management. Growth data on these species have been extensively collected in the USSR. Many of these studies involved measuring growth between marks made on the podetium (e.g. Gorodkov, 1936; Glinka, 1939; Igoshina, 1939) and have been summarized by Andreev (1954). Similar studies in North America have been pioneered by Ahti (1959), Scotter (1963) and Pegau (1968). The latter has shown that the growth rate of *Cladonia alpestris*, *C. rangiferina* and *C. sylvatica* in Alaska is remarkably similar and varies between 4 and 6 mm annual linear increase. In the USSR, Andreev (1954) recorded similar rates but these may be as low as 2.7 mm $year^{-1}$ in *C. rangiferina.* The internode between branches is believed to represent 1 year's growth, so that the age of the podetium may be estimated by dividing the number of nodes into the total height (Scotter, 1963; Kärenlampi, 1970). Kärenlampi (1971) investigated several climatic factors that would be expected to influence growth rate and he showed that water availability was more influential than temperature or light intensity. Kershaw and Rouse (1971) have shown that the mean podetial length, internode length and podetial diameter of *C. alpestris* are greater in areas of high soil moisture content than in drier habitats, and Lindsay (1975) has attributed the relatively high rate of growth of *C. rangiferina* (5.33 mm $year^{-1}$) on the cold oceanic sub-Antarctic island of South Georgia to the high precipitation. The majority of published studies on the growth of these lichens relate to linear increases. However, Lindsay (1975) obtained weight increases by *C. rangiferina* on South Georgia of 49–62 mg g^{-1} dry weight over 100 d during the main summer growth period. Similarly, in Finland, during 114 d in summer, weight increases of 80 mg g^{-1} dry weight have been recorded in the top 5 cm of thalli of *Cetraria nivalis* (Kärenlampi and others, 1975), a species ecologically similar to *C. rangiferina.*

In this paper, growth by weight increase is presented for two terricolous fruticose lichens on Signy Island, South Orkney Islands. The study was conducted at the same time as experiments were performed on South Georgia (Lindsay, 1975), such that the productivity of *C. rangiferina* in the sub-Antarctic and maritime Antarctic could be compared. The communities of lichens and bryophytes on Signy Island in which *C. rangiferina* and *S. globosus* are components have been described by Smith (1972). Both species are associated with the tall turf-forming mosses *Chorisodontium aciphyllum* and *Polytrichum alpestre* with *S. globosus* being abundantly distributed on the latter. Although other *Cladonia* spp. are often abundant on these mosses, *C. rangiferina* is comparatively rare on Signy Island. The colonies are usually much stunted and the severe climate on Signy Island, where the mean air temperature for the warmest month (January) is only 0.9°C, suggest that the species is near the southern limit of its

* Present address: 11 Bramley Close, Cadbury Farm, Yatton, Bristol BS19 4JY.

geographical distribution (the farthest south occurrence is in the South Shetland Islands (Lindsay, 1971; as *Cladonia vicaria*).

Materials and Methods

Material of *Cladonia rangiferina* var. *vicaria* (R. Sant.) Ahti and *Sphaerophorus globosus* (Huds). Vain. was collected on Signy Island (lat. 60°43′S, long. 45°38′W) from north-facing moss banks formed by *Chorisodontium aciphyllum* and *Polytrichum alpestre* at 50 m altitude on Observation Bluff. Further material of *C. rangiferina* was collected from lichen-rich *Festuca contracta* grassland at 30 m above King Edward Cove, Cumberland East Bay, South Georgia (lat. 54°17′S, long. 36°30′W). This latter material was kept at −20°C for 4 weeks before use.

Methods of measuring the growth of these fruticose lichens initially followed that of Lindsay (1975), being based on the method of Kärenlampi (1971) but, due to the exceedingly slow rate of growth on Signy Island, improved methods were subsequently developed. Those of Andreev (1954) and Pegau (1968) for measuring linear growth of podetia were not employed due to difficulties of marking the podetia in the field with sufficient accuracy to resolve growth at an anticipated rate of 1 mm year^{-1} or less.

Thirty-six containers for cores, comprising aggregates of podetia (20–40 mm deep), were constructed of short perspex cylinders 100 mm in diameter by 50 mm deep with fine wire mesh glued across one end to allow throughfall of precipitation (Lindsay, 1975). All the dead or decaying basal parts of the podetia were cut away so that the containers supported only the living assimilating tissues. To simulate natural conditions, the containers were sunk 50 mm into moss banks of mixed *Polytrichum alpestre* and *Chorisodontium aciphyllum* (Fig. 1). Six samples were set out thus in each of six different sites, varying in aspect (north- and south-facing) and altitude (15–100 m a.s.l.). At each site, three of the containers supported lichen from South Georgia. This method, however, was found to be unsuitable on Signy Island, because the containers accumulated wind-blown detritus and the wire mesh rusted and may have affected growth. In subsequent experiments the wire mesh was replaced with nylon gauze covering both top and bottom of the containers, enclosing the lichen, and the base of the container was additionally covered with polythene to prevent possible loss of fragmented podetia but also maintaining drainage of rain water. Use of smaller containers 50 mm in diameter by 30 mm deep was also explored but in all cases growth measurements proved to be erroneous by weight loss.

In order to secure more reliable data, individual podetia were placed in small glass tubes 50 mm long by 5.5 mm internal diameter. The basal 10 mm of the tube was plugged with absorbant tissue paper to prevent the podetium falling through the tube, whilst also conveying moisture and nutrients to the specimen. The tubes containing the lichens were pushed 40 mm into the moss turves from where they had been originally collected (Fig. 2). Sixty podetia of

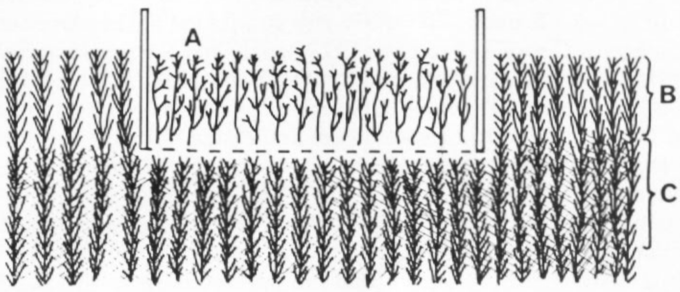


Fig. 1. Diagram showing open perspex container with wire mesh base containing podetia of *C. rangiferina* (A), sunk into the moss turf amongst the assimilating stems (B) above the non-assimilating peaty sub-surface (C).

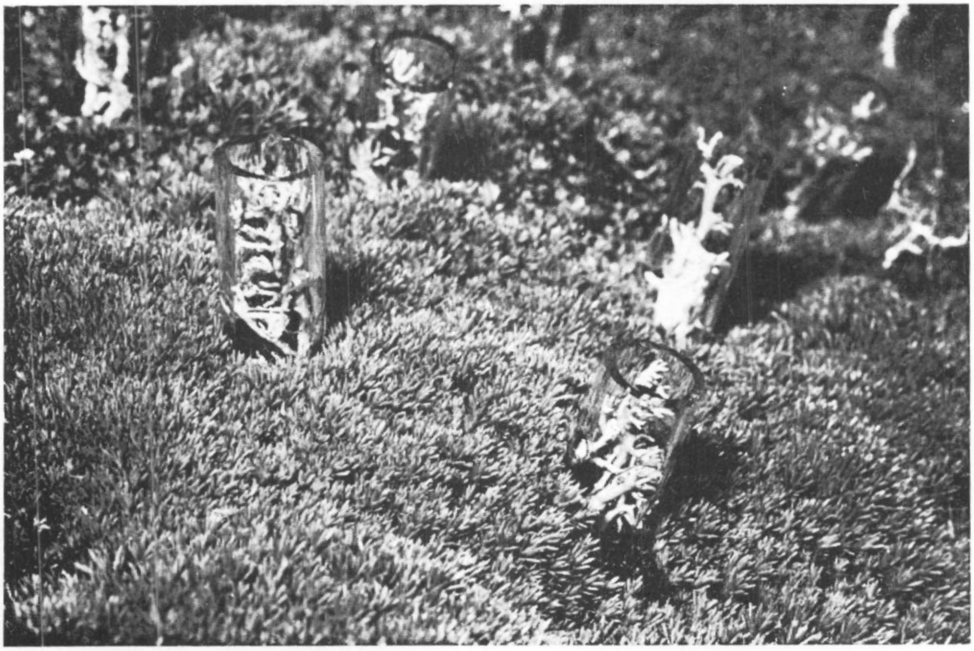


Fig. 2. Single podetia of *Sphaerophorus globosus* in glass tubes in the moss *Polytrichum alpestre*.

C. rangiferina and 40 podetia of *S. globosus* were studied at three sites of differing altitude, namely 15, 50 and 100 m a.s.l. on the north-facing slope of Observation Bluff. Twenty podetia of each species were studied at the high and low sites and a further 20 *Cladonia* podetia were grown on the 50 m site. Specimens were air dried for 10 d at 18°C in the laboratory, then weighed to an accuracy of 0.1 mg. Prior to subsequent weighing, the podetia were individually washed before and after the experimental periods to remove all extraneous matter.

In addition, three colonies of *S. globosus*, 6, 30 and 130 mm in diameter, were photographed over a 26 month period on Signy Island. The photographs were examined for colony expansion and podetial growth.

Results

Experiments on the growth rate of aggregates of podetia of both species in containers were largely inconclusive due to fragmentation and loss of branches, and erroneous weight gains resulting from wind-blown detritus. Following the initial method of Lindsay (1975), using open containers (100 mm in diameter with wire mesh bases), at the end of the growth period (20 January–24 February 1972) only 18 of 36 samples had gained weight (maximum 0.71 g = 62.86 mg g^{-1} dry weight) with no recognizable difference in behaviour between Signy Island and South Georgian material. The mean gain for samples from Signy Island and South Georgia was respectively 20.99 and 21.32 mg g^{-1} dry weight (standard error for the total sample was 6.95). All other samples had lost weight in varying amounts (maximum 1.62 g = 120 mg g^{-1} dry weight). Completely enclosing the specimens in the containers did not improve the experimental technique. All such specimens lost weight. Using smaller containers (50 mm in diameter) was also unsatisfactory. Despite a prolonged growth period spanning the summer and autumn (28 December 1972–8 April 1973), there was weight loss from all 30 samples of *C. rangiferina* and all 20 samples of *S. globosus*.

Productivity studies on the individual podetia in glass tubes were more successful. The micro-environment was more protected and moist, and the cleanliness of the specimens could be maintained throughout the growth period (27 November 1973–18 March 1974). Of the initial 100 individual podetia (all Signy Island material), 12 had been lost by wind but the remaining 88 had all gained weight by the end of the growth period. However, a mid-season weighing on 9 January 1974 indicated that half of the lichens had decreased very slightly in weight or remained unchanged (Table I). Much of the growth occurred between January and March. There was no statistically significant (*t*-test) difference between productivity at differing altitudes above sea-level in either species. In *Cladonia*, production appeared to increase slightly with increasing altitude. The mean obtained for the entire experimental period (119 d), for all altitudes, was 84.4 mg g^{-1} dry weight (maximum for a single podetium 16.3 mg g^{-1} dry weight). *Sphaerophorus* grew more slowly and production decreased at the higher altitude (mean 34.1 mg g^{-1} dry weight, maximum 90.9 mg g^{-1} dry weight).

Figs 3 and 4 show that production relative to podetium size (weight) is extremely variable but there was a general trend for production to be greater in the larger podetia which, being more richly branched, presented more growing apices. This correlation was statistically significant in only three samples, viz. *C. rangiferina* at 15 m (1% *P*), 100 m (5% *P*) and *S. globosus* at 15 m (1% *P*).

The rate of growth of *C. rangiferina* and *S. globosus* has also been expressed in terms of replacement period. The podetia of these lichens grow continuously upward with the basal

TABLE I. MEAN PRODUCTION OF SINGLE PODETIA (n = 20) OF *Cladonia rangiferina* AND *Sphaerophorus globosus* THROUGHOUT THE SPRING AND EARLY SUMMER, AND LATE SUMMER AND AUTUMN

Site altitude (m a.s.l.)	*Mean podetium weight* (mg)	*Mean relative productivity* (mg g^{-1} dry wt) 27 Nov. 1973– 9 Jan. 1974	9 Jan.– 26 Mar. 1974	Annual growth year	*Replacement period* (years)
Cladonia rangiferina					
15	20.9	7.45	70.81	78.26	14
50	21.3	−0.42	85.90	85.48	11
100	22.8	21.11	68.40	89.51	15
Sphaerophorus globosus					
15	20.6	6.20	38.30	44.50	23
100	18.7	−3.50	29.90	26.40	33

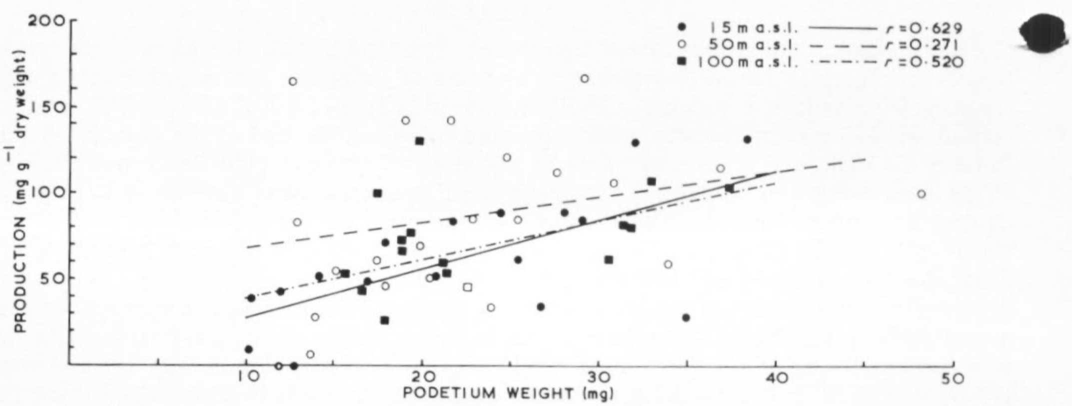


Fig. 3. Production of *Cladonia rangiferina*.

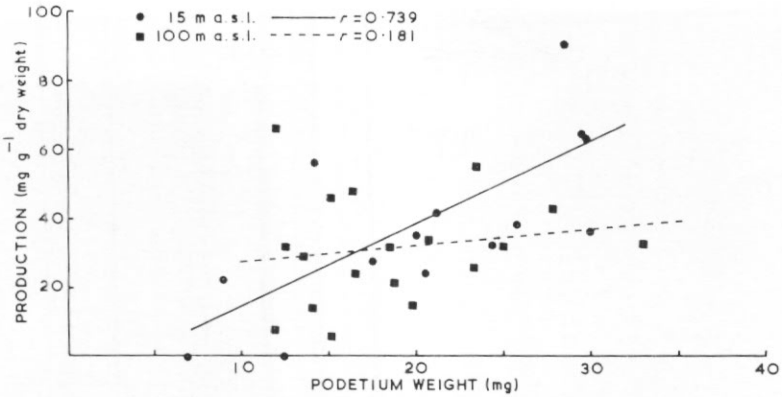


Fig. 4. Production of *Sphaerophorus globosus*.

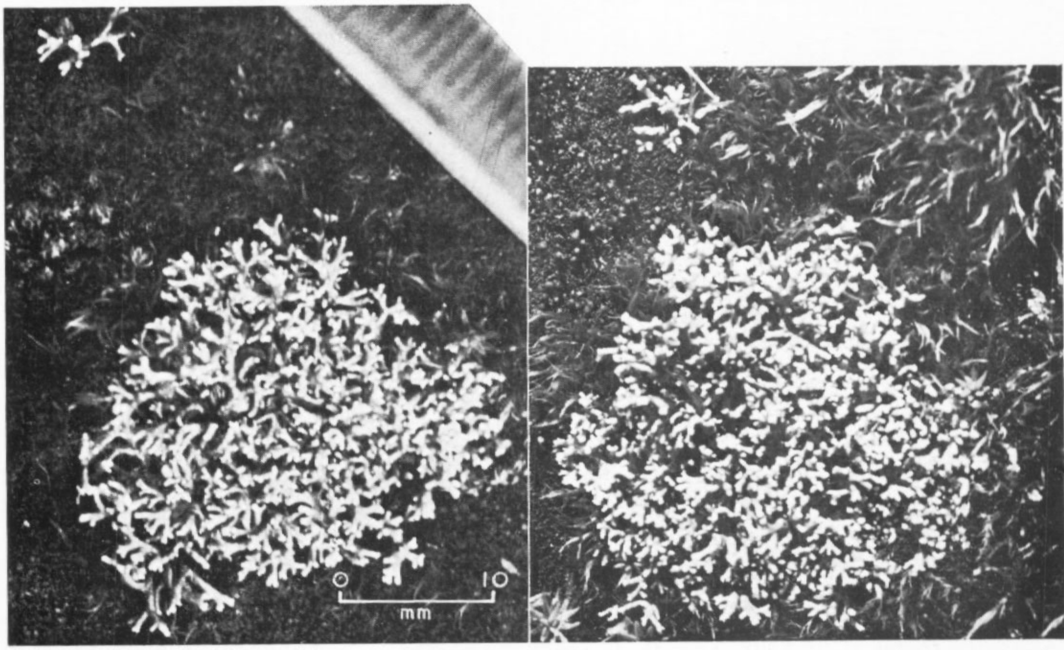
portion dying away. The replacement period is therefore a measure of the age of the living assimilating tissue, and it is shown (Table I) that the more rapidly growing podetia have shorter replacement periods because the overall weight of the podetium is relatively constant. The mature podetium is thus in a state of equilibrium (Ahti, 1961), making it essential in these studies initially to remove the necrotic basal portions if any weight increase is to be accurately measured. The replacement periods for *C. rangiferina* and *S. globosus* on Signy Island are estimated to be 11–15 years and 23–33 years, respectively. Although this expression refers only to the age of the living portions, Ahti (1961) (summarizing Andreev (1954)) has indicated that podetia of *C. alpestris*, *C. arbuscula* agg. and *C. rangiferina* may have a total life span of 100–150 years. Comparable data for *S. globosus* are not available.

Photographs of colonies of *S. globosus* over two and a half growing seasons (1971–72 to 1973–74) revealed that podetia in a juvenile colony (6 mm in diameter) have a linear increase of 0.5–0.8 mm year^{-1}, but that in a larger colony (30 mm in diameter) the rate of linear growth increases to 2 mm year^{-1} (Fig. 5). An older colony (130 mm in diameter) showed no lateral expansion and was beginning to be enveloped by extrusive growth of *Polytrichum alpestre*.

Discussion

Growth experiments on Signy Island using aggregates of podetia in containers were completely unsuccessful even though identical procedures achieved satisfactory results on South Georgia (Lindsay, 1975). Specimens were "vandalized" by brown skuas, lost during gales, experienced weight loss by wind erosion or weight gains by accumulation of wind-blown debris. Measurements on single podetia of *C. rangiferina* in glass tubes embedded in moss turves gave a mean growth rate of 84.4 mg g^{-1} dry weight over a period of 119 d, spanning most of the summer growth period of crustose lichens on Signy Island (Hooker, 1980*a*). This value is higher than that obtained on South Georgia by Lindsay (1975), who recorded 62 and 49 mg g^{-1} dry weight at altitudes of 30 and 150 m a.s.l., even when taking into account the shorter growth period (100 d) in Lindsay's experiment. This is surprising as Signy Island experiences a considerably more severe climate than South Georgia. Much of the precipitation occurs as snow (Smith, 1972), temperatures are lower and the growing season is effectively shorter. The greater productivity of *C. rangiferina* measured on Signy Island is probably due to prolonged moisture retention by the podetia in the glass tubes which, additionally, may have given rise to a warmer "green-house" effect.

Both species demonstrated a pattern of seasonal growth. Maximum growth occurred during the summer and autumn with very little, if any, growth occurring during the spring. This



a b

Fig. 5. Growth of two colonies of *Sphaerophorus globosus*, 6 mm and 30 mm in diameter. a. December 1971; b. March 1974.

pattern has also been shown in crustose lichens on Signy Island (Hooker, 1980*a*) and the delayed resumption of growth following the relatively severe polar winter (when air temperatures may fall to −40 °C at sea-level on Signy Island) has been correlated with reduction of photosynthetic rate and loss of net carbon assimilation; leakage of cellular cations and soluble carbohydrates; break-down of soluble carbohydrate reserves and loss of soluble carbohydrate transfer between the symbionts (Hooker, 1977). Gannutz (1970) inferred a critical reduction of metabolic storage products in Antarctic lichens during the spring following the harsh winter at the Argentine Islands, Antarctic Peninsula, where field respiratory studies in the Antarctic revealed that nocturnal respiration may be non-existent during the spring in the absence of respirable substrate.

The pattern of linear growth rate seen in young, mature and old colonies of *S. globosus* is similar to that described for other fruticose lichens, e.g. *Cladonia* spp. (Andreev, 1954) (summarized by Ahti (1961)), and Antarctic saxicolous *Usnea* spp. (Hooker, 1980*b*) in which growth is initially slow, increasing to a maximum rate in mature thalli and then decreasing with old age, this also having been demonstrated in crustose lichens (Hale, 1973; Armstrong, 1976). Because *C. rangiferina* and *S. globosus* grow so slowly, the question arises how they can maintain themselves amongst mosses which grow more rapidly. Individual podetia of *Cladonia furcata* are commonly found growing on moss banks of *Chorisodontium aciphyllum* and may be traced downwards through the turf to a depth of 40–50 mm. Since the moss grows at an annual rate of 3–7 mm but may exceed 10 mm in favourable habitats (Baker, 1972; Collins, 1976), it is presumed that this lichen must grow at an equivalent rate. However, with *C. rangiferina* and *S. globosus*, in which the podetia are usually aggregated into colonies, the concept is presented of a "floating" colony. Examination of the base of aggregates of these two species showed an interwoven mass of dead podetia fragments supporting the living portions, and that the whole colony appeared to gain lateral support from the moss. It is thus envisaged that as the moss grows upwards the lichens are raised as a whole, and that the dead basal portions become torn away (perhaps while still frozen into the moss peat) and are left behind. In this manner, colonies of the slow-growing fruticose lichens could be maintained in an almost floating situation on the moss banks for many years, at least for the duration of the replacement period, which for podetia 30 mm tall of *C. rangiferina* and *S. globosus* would represent an equivalent growth of the surrounding mosses of 30–100 mm and 70–230 mm, respectively. It is more difficult to understand how the lichens initially become established as their extension growth may be 0.5 mm year^{-1} or less. On Signy Island, colonies of *Cladonia* spp. and *S. globosus* are commonly found on shallow stands (20–30 mm deep) of coalesced cushions of *Andreaea* spp. (Smith, 1972), a primary colonizer of exposed mineral soil. This situation is favourable to the lichen, because, due to the rate of moss growth being more or less balanced by the rate of basal decay, the depth of the stands is uniform. This community may be invaded by *Chorisodontium aciphyllum* but, since most plant communities on Signy Island appear to be climax units with only occasional evidence of successional stages (Smith, 1972), there is no evidence available to suggest that the lichens become established on *Andreaea* prior to successional colonization by the peat-forming mosses, by which time the mature podetia will have attained their maximum rate of growth and can compete with the rapid moss growth. To resolve this question, detailed studies are required on the duration of the lichen life span and the rate of linear growth of juvenile, mature and old podetia in all moss communities in which these lichens occur.

ACKNOWLEDGEMENTS

I am indebted to Dr R. I. L. Smith for supervising field studies; to Dr D. H. Brown, Department of Botany, University of Bristol, for valuable comments on an earlier draft of this paper, and to Professor D. C. Smith for facilities in the Department of Botany, University of Bristol.

MS received 15 December 1978

REFERENCES

AHTI, T. 1959. Studies on the caribou lichen stands of Newfoundland. *Suomal. eläin- ja kasvit. Seur. van. kasvit. Julk.*, **30,** No. 4, 44 pp.

———. 1961. Taxonomic studies on reindeer lichens (*Cladonia* subgenus *Cladina*). *Suomal. eläin- ja kasvit. Seur. van. kasvit. Julk.*, **32,** No. 1, 160 pp.

ANDREEV, V. N. 1954. Prirost kormovikh lishainikov i priyomy yago regulirovaniya [Growth of forage lichens and methods for their regulation]. *Trudÿ bot. Inst. Akad. Nauk SSSR*, Ser. 3, **11,** 9–74.

ARMSTRONG, R. A. 1976. Studies on the growth rate of lichens. (*In* BROWN, D. H., HAWKSWORTH, D. L. *and* R. H. BAILEY, *ed. Lichenology: progress and problems.* London and New York, Academic Press, 309–22.)

BAKER, J. H. 1972. The rate of production and decomposition of *Chorisodontium aciphyllum* (Hook. f. & Wils.) Broth. *British Antarctic Survey Bulletin*, No. 27, 123–29.

COLLINS, N. J. 1976. The development of moss-peat banks in relation to changing climate and ice cover on Signy Island in the maritime Antarctic. *British Antarctic Survey Bulletin*, No. 43, 85–102.

GANNUTZ, T. P. 1970. Photosynthesis and respiration of plants in the Antarctic Peninsula region. *Antarct. Jnl U.S.*, **5,** No. 1, 49–52.

GLINKA, D. M. 1939. [The seasons of reindeer pastures and significance of green forage in winter-feeding of reindeer in Nanets District]. *Leningr. Ser. Olenov.*, **4,** 31–46. [In Russian.]

GORODKOV, B. N. 1936. [A study of the growth of lichens]. *Sov. Olenov.*, **8,** 87–115. [In Russian.]

HALE, M. E. 1973. Growth. (*In* AHMADJIAN, V. *and* M. E. HALE, *ed. The lichens.* New York and London, Academic Press, 473–92.)

HOOKER, T. N. 1977. *The growth and physiology of Antarctic lichens.* Ph.D. thesis, University of Bristol, 188+10 pp. [Unpublished.]

———. 1980*a*. Factors affecting the growth of Antarctic crustose lichens. *British Antarctic Survey Bulletin*, No. 50, 1–19.

———. 1980*b*. Growth and production of *Usnea antarctica* and *U. fasciata* on Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, No. 50, 35–49.

IGOSHINA, K. N. 1939. [The growth of forage lichens on the Ural North]. *Leningr. Ser. Olenov.*, **4,** 7–29. [In Russian.]

KÄRENLAMPI, L. 1970. Morphological analysis of growth and productivity of the lichen *Cladonia alpestris*. *Rep. Kevo Subarct. Res. Stn*, **7,** 9–15.

———. 1971. Studies on the relative growth rates of some fruticose lichens. *Rep. Kevo Subarct. Res. Stn*, **7,** 33–39.

———, TAMMISOLA, J. *and* H. HURME. 1975. Weight increase of some lichens as related to carbon dioxide exchange and thallus moisture. (*In* WIELGOLASKI, F. E., *ed. Fennoscandian tundra ecosystems. Part 1. Plants and microorganisms*. Berlin, Springer-Verlag, 135–37.) (Ecological studies, No. 16.)

KERSHAW, K. A. *and* W. R. ROUSE. 1971. Studies on lichen dominated systems. II. The growth pattern of *Cladonia alpestris* and *Cladonia rangiferina*. *Can. J. Bot.*, **49,** No. 8, 1401–10.

LINDSAY, D. C. 1971. Vegetation of the South Shetland Islands. *British Antarctic Survey Bulletin*, No. 25, 59–83.

———. 1975. Growth rates of *Cladonia rangiferina* (L.) Web. on South Georgia. *British Antarctic Survey Bulletin*, No. 40, 49–53.

PEGAU, R. 1968. Growth rates of important reindeer forage lichens on the Seward Peninsula, Alaska. *Arctic*, **21,** No. 4, 255–59.

SCOTTER, G. W. 1963. Growth rates of *Cladonia alpestris*, *C. mitis*, and *C. rangiferina* in the Taltsen River region, N.W.T. *Can. J. Bot.*, **41,** No. 8, 1199–202.

SMITH, R. I. L. 1972. Vegetation of the South Orkney Islands with particular reference to Signy Island. *British Antarctic Survey Scientific Reports*, No. 68, 124 pp.