# GROWTH AND PRODUCTION OF *Usnea antarctica* AND *U. fasciata* ON SIGNY ISLAND, SOUTH ORKNEY ISLANDS

*By* T. N. HOOKER*

ABSTRACT. Direct measurements of *U. antarctica* showed a net annual production of approximately 40 mg g$^{-1}$ dry weight year$^{-1}$ in the mature thallus, but production by juvenile thalli (less than 0.5 g dry weight) can be as great as 150 mg g$^{-1}$ dry weight year$^{-1}$. Net annual production of mature thalli of *U. fascita* (more than 0.5 g dry weight) was approximately 35 mg g$^{-1}$ dry weight year$^{-1}$. Lichenometric data for juvenile thalli growing on pebbles and timbers, and for very old thalli on moraines, provided values of net annual production of, respectively, 50–200 mg g$^{-1}$ dry weight year$^{-1}$ and 1–5 mg g$^{-1}$ dry weight year$^{-1}$. Some evidence is presented suggesting that in very old thalli, 300–600 years old, net annual productivity continues to decrease. Photographic studies of *U. antarctica* revealed a branch extension rate of 0.45 mm year$^{-1}$.

THE complex morphology of fruticose lichens, especially *Usnea* spp., does not easily lend itself to studies of growth and productivity. Most work on fruticose lichens has been on species of "reindeer lichens", especially *Cladonia rangiferina* and related species (Andreev, 1954; Pegau, 1968; Kärenlampi, 1971; Lindsay, 1975; Hooker, 1980*b*). The growth of other species of fruticose lichens has received little attention. Hooker (1980*b*) has studied production in *Sphaerophorus globosus* on Signy Island, South Orkney Islands, and Herre (1904) showed that the arboreal lichen *Ramalina reticulata*, which may attain a length of up to 2 m, can grow between 11 and 90 mm during the 7 months of Californian winter, probably the main growth period. Lindsay (1973) provided some estimates of productivity for *Usnea antarctica* on Signy Island by lichenometrically determining the growth of thalli that had colonized timbers of approximately known age. Although in the absence of more reliable data such information is interesting, it has to be emphasized that the methodology is potentially erroneous (Lindsay, 1973). No knowledge is available on the length of the weathering period of the substratum prior to lichen colonization (i.e. the age of the specimen is never known with accuracy) and it is additionally necessary to assume that the growth rate is always linear throughout the lichen life span, an assumption without good justification (Hale, 1973; Armstrong, 1976). Furthermore, in Lindsay's work, timber is an artificial substratum for *U. antarctica*, there being no woody plants in the maritime Antarctic.

This paper attempts to present a more accurate assessment of the growth and net annual production of *U. antarctica* and *U. fasciata* on Signy Island (lat. 60°45′S, long. 43°38′W) in the maritime Antarctic. Such information, together with the productivity studies on the island's dominant moss species (Baker, 1972; Collins, 1973, 1976, 1977) is essential for assessing the mean net primary productivity of Signy Island. *Usnea antarctica* and *U. fasciata* comprise the dominant vegetation in many of the more rocky and exposed habitats on the island and in many areas they provide 100% coverage of boulders, cliffs and other rock surfaces, and also stable areas of mineral soil and glacial debris (Gimingham and Smith, 1970; Smith, 1972). *U. antarctica* is also a frequent epiphyte on *Polytrichum alpestre–Chorisodontium aciphyllum* banks, and locally a densely branched pale yellow form provides extensive cover on some banks. It also occurs occasionally amongst other mosses. However, *U. fasciata* is never found as an epiphyte, although it may be attached to stones or boulders embedded in moss stands. The plant ecology, geographical and climatic features of Signy Island have been described by Holdgate (1967) and Smith (1972).

## METHODS

Due to the exceedingly slow rate of growth of *Usnea* spp. on Signy Island, various methods were employed to determine growth and productivity in this taxon. These methods involved

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direct measurement of growth over periods of up to 28 months and determination of productivity in lichenometrically dated specimens.

*Direct measurement*

The methods that have been developed for measuring growth and productivity in terricolous fruticose lichens, in particular *Cladonia* spp. (Andreev, 1954; Pegau, 1968; Kärenlampi, 1970; Lindsay, 1975; Hooker, 1980*b*) are not applicable to individual thalli of saxicolous fruticose species. Various methods were therefore developed for studying growth by dry-weight increase in addition to linear increase of branch length.

*Weight increases.* Mature thalli (more than 0.5 g dry weight) were collected from Observation Bluff, Signy Island, by scraping the thallus holdfast cleanly from the rock surface. Since this extremely hard organ serves for attachment only, having no apparent function in thallus water relations, it was considered that this procedure would not jeopardize the performance of the lichens in experimental conditions. Thalli were thoroughly washed to remove particles of soil, fragments of moss and the alga *Prasiola crispa*, and broken branches of *Usnea*, air dried and weighed to the nearest 0.1 mg at the beginning and end of the experimental periods. The following methods of exposing thalli in the field were employed:

i. Thalli of *U. antarctica* were grown on a bed of natural mineral soil and pebbles contained in seed trays and securely tethered by strong cotton thread tied to the base of the trays. Four trays, each containing 12 thalli, were prepared and set out on the north-facing slope of Observation Bluff (3 January 1972–14 February 1972) at intervals of approximately 30 m altitude (30–120 m a.s.l.).
ii. Thalli of *U. antarctica* and *U. fasciata* were set out in specific moss communities in which they naturally occur. Small plastic cylinders, 4 cm in diameter by 3 cm deep, were prepared from polythene sample bottles. Nylon gauze was glued on to the top of each cylinder and a single lichen thallus was tied to the gauze. The cylinder was then firmly pushed into stands of *Andreaea regularis*, *Chorisodontium aciphyllum*, *Drepanocladus uncinatus* and *Polytrichum alpestre* such that the gauze lay securely across the surface of the moss and the attached lichen was in close contact with the moss (Fig. 1). Sixty thalli of each species were thus set out in six different sites between 6 February 1972 and 9 March 1972.
iii. Thalli of *U. antarctica* and *U. fasciata* were maintained in their natural state attached to pebbles of quartz-mica-schist. All thalli but one were removed from each pebble while those of crustose lichens, although few, were removed by scraping with a knife. The specimens were washed, weighed after air drying in the laboratory for several days and returned to their original habitats on bare mineral soil (15 and 75 m a.s.l. on the north side of Observation Bluff) adjacent to areas densely colonized by *U. antarctica*. Each specimen was identified by a small numbered wooden stake (Fig. 2). A total of 80 individual thalli was thus measured. The experimental growth period (5 December 1973–9 March 1974) covered the main growing season of terricolous fruticose lichens (Hooker, 1980*b*) and crustose lichens (Hooker, 1980*a*) on Signy Island and thus it is anticipated that these data reflect the complete annual productivity.

The desiccation rate of *Usnea* was studied to reduce possible errors when dry weighing thalli. The fully saturated thallus of *U. antarctica* required 6 days before constant weight was achieved at room temperature (18 °C). In experiments where the thallus remained attached to a pebble, constant air-dry weight in the laboratory was still not attained within 27 d of initial saturation. This was probably due to water retention in the laminae of the quartz-mica-schist. Although the specimens (lichen and pebble) were still losing approximately 0.3 mg $d^{-1}$ after 20 d, the loss was sufficiently regular to enable accurate weighings to be made.

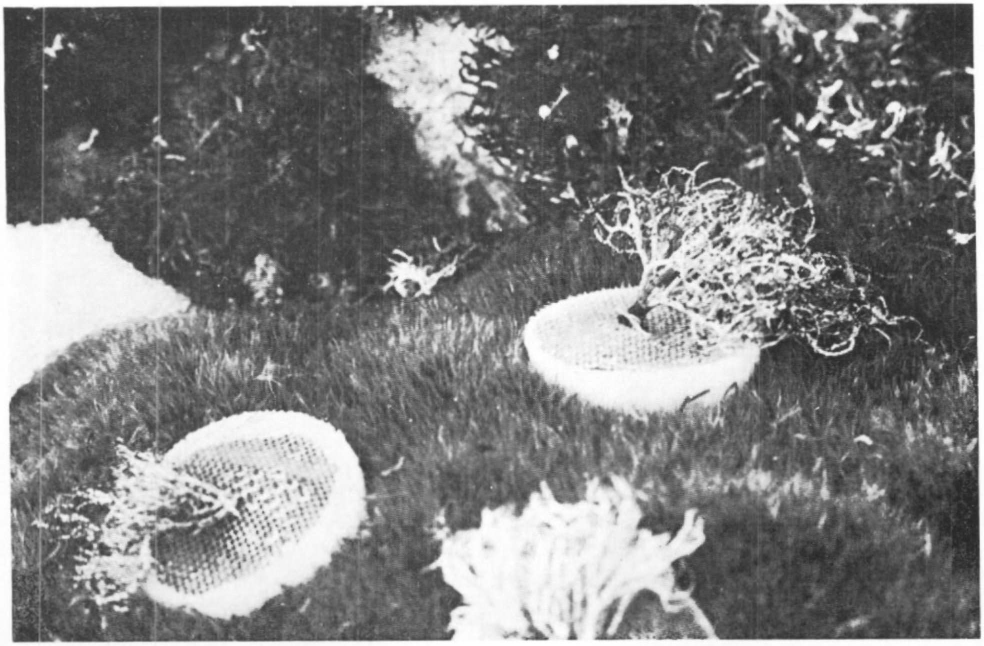


Fig. 1. Thalli of *Usnea antarctica* tied on to nylon gauze and anchored to moss turf (*Chorisodontium aciphyllum*

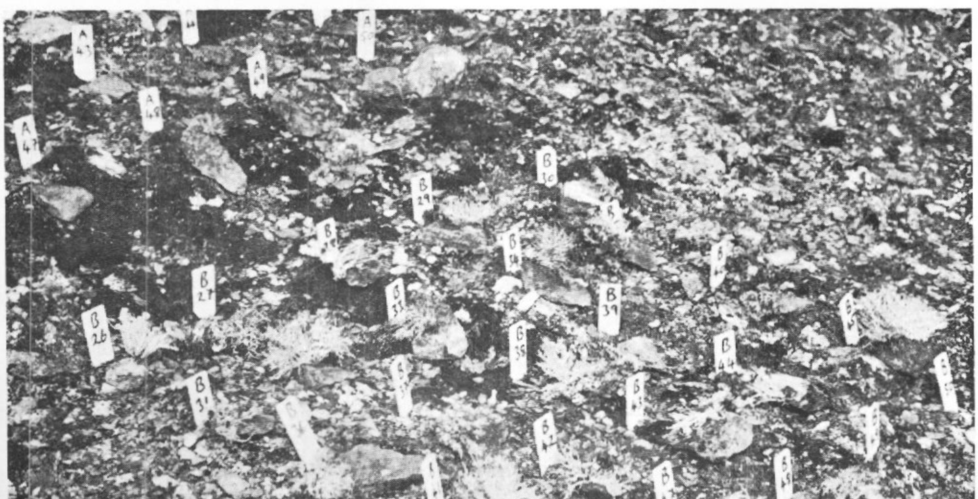


Fig. 2. Thalli of *Usnea fasciata* attached to pebbles on mineral soil.

*Linear increase of branches.* Measurements of extension growth of individual branches of *U. antarctica* were attempted by macro-photography. Ten individual thalli at each of seven sites (15–105 m a.s.l., at intervals of approximately 15 m altitude) were monitored on Observation Bluff in both rock and moss habitats. Individual branches on each thallus, together with a millimetre scale, were photographed during dry weather at monthly intervals from December 1971 to February 1972 and again in March 1974. Measurements were made from the photograph using mathematical dividers, and the natural green-black variegated markings along the branches provided points for reference.

Of the two methods of direct measurement employed, greatest emphasis is placed on weight gain, since this can be used for productivity and age determinations. Length is less easily equated with production and even age, because thallus growth form is apparently modified by habitat factors.

*Indirect measurements*

The growth and net annual production of *Usnea* spp. has also been estimated in thalli of lichenometrically determined age. Thalli studied in this manner were collected from several moraines in Moraine Valley adjacent to Orwell Glacier, below the island's ice cap inland from Port Jebsen, and close to Sombre Lake; other thalli were on pebbles from former nests of giant petrels abandoned about 1954, and some were derived from timbers associated with buildings of known age. (Detailed lichenometric assessment of the moraines on Signy Island will be presented in a separate paper, but for clarity it is reported here that the numbers of moraines associated with Orwell Glacier, Sombre Lake and near Port Jebsen are 12, 2 and 4, respectively, and the numbering used here follows that of Hooker (1977).) Estimated ages of thalli found on the moraines have been assessed using the crustose lichen *Rhizocarpon geographicum*, the growth rate of which on Signy Island moraines has been determined as 10 mm in diameter per century (Hooker, 1980*a*). By plotting thallus dry weight of the heaviest and presumably oldest thalli of *Usnea* spp. against the dates of moraine colonization by *R. geographicum*, the slope of the graph provides an estimation of the growth rate of *Usnea*. Usually as many as 50 individual thalli were collected and dry weighed from each site or substratum but, where colonization was sparse, the sample number was less. This, however, does not affect the final analysis because the data have to be based on the single observed maximum size (and theoretically oldest) lichen found.

## Results

*Direct measurements*

In all experiments where thalli of *Usnea* had been detached from their substratum, most specimens lost weight, presumably by wind abrasion and fragmentation. This amounted to as much as 88% of the lichen being lost, rendering all results inconclusive. Of 168 thalli only 11 gained weight (maximum 0.109 g = 118.6 mg $g^{-1}$ dry weight).

Thalli of *U. antarctica* and *U. fasciata* attached to pebbles produced more successful results but fragmentation still posed a problem, and of 80 individual thalli only 34 demonstrated a weight gain (Figs 3 and 4). Thus, even the positive values recorded may be underestimates of the true growth, particularly the lower values, and all estimates of production need to be based on the maximum recorded values.

Within these severe limitations, it is shown that juvenile thalli of *U. antarctica* (less than 0.5 g dry weight) have a net annual production (mg $g^{-1}$ $year^{-1}$) greater than larger older thalli (more than 0.5 g dry weight), the net annual production of the latter being 40 mg $g^{-1}$ dry weight $year^{-1}$ (Fig. 3). With *U. fasciata* (Fig. 4), the thalli measured were larger than 0.5 g dry weight and the productivity was apparently linear and at approximately the same rate achieved by "mature" thalli of *U. antarctica*.

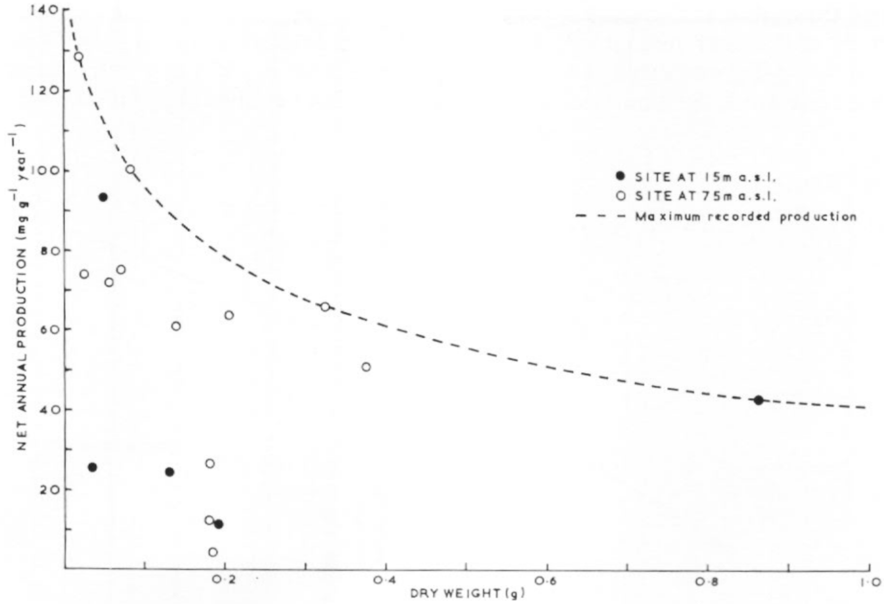



Fig. 3. Net annual production of *Usnea antarctica* grown on pebbles.

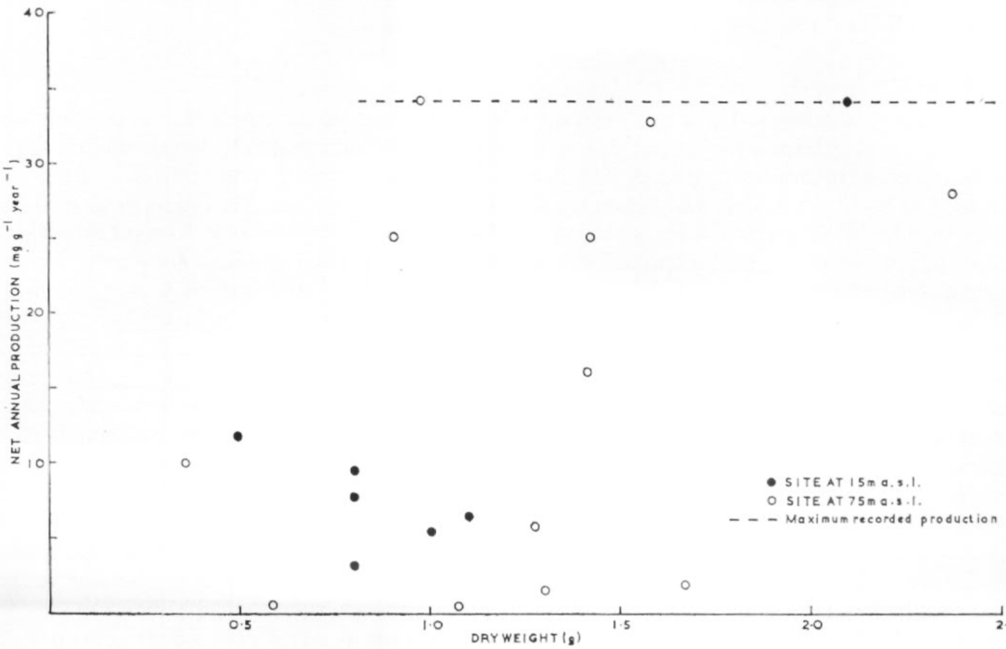



Fig. 4. Net annual production of *Usnea fasciata* grown on pebbles.

Based on these observations, it has been possible to develop a graph of the estimated weight gain of thalli of *U. antarctica* during the first 200 years of its life span (Fig. 5). For example, a thallus of 0.1 g dry weight has a net annual production of *c.* 100 mg $g^{-1}$ dry weight $year^{-1}$ (Fig. 3) and thus would be estimated to be 10 years old. The net annual production of a thallus

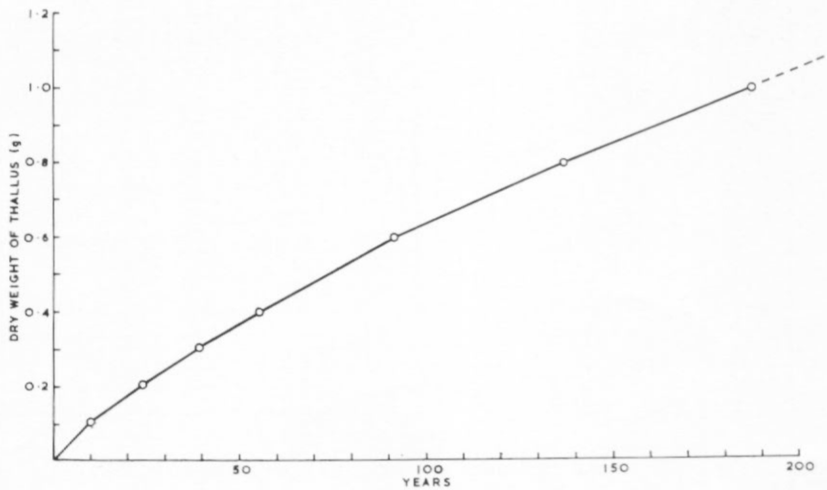



Fig. 5. Age–weight relationship of *Usnea antarctica* grown on pebbles.

0.2 g dry weight is *c.* 70 mg $g^{-1}$ dry weight $year^{-1}$ (Fig. 3), thus approximately 14 years would be required to achieve a weight gain of 0.1 g, making the 0.2 g dry weight thallus approximately 24 years old, etc. The "juvenile" growth rate of *U. fasciata* is not known but may be expected to follow a similar pattern for that of *U. antarctica.*

*Indirect measurements*

*Colonization of moraines.* Data are presented here only for those moraines supporting both *Usnea* spp. and *Rhizocarpon geographicum*, since it was only possible lichenometrically to date lichen colonization of moraines supporting *R. geographicum*. Estimated dates of moraine colonization by *R. geographicum* based on the photographically recorded growth rate of that species on Orwell Glacier moraines (Hooker, 1980*a*) are shown in Table I together with the maximum dry weight of *Usnea* spp. on the moraines, their rate of growth (mg $year^{-1}$) and net annual production (mg $g^{-1}$ dry weight $year^{-1}$), assuming that colonization was synchronous with that of *R. geographicum.* This assumption is, however, difficult to justify and the probability for colonization to have been successional must be greater than that for synchrony of species establishment on the moraines, and this is supported by the data given below. Quantitatively, of the 26 moraines examined 15 were colonized by *Usnea* spp. and nine by *R. geographicum*, and this might be interpreted as an indication for *Usnea* to colonize prior to *R. geographicum*. However, if colonization is successional between these species, it may be considered that the temporal distance between the succession will be constant. Therefore, by plotting maximum thallus size of *Usnea* against the date of moraine colonization by *R. geographicum*, the slope of the graph should provide a more accurate measure of the annual growth rate of *Usnea* spp. (Fig. 6 and Table I). This procedure demonstrates that the origins of the graphs for *Usnea* and *R. geographicum* do not coincide (as would be the case for synchronous colonization) and that on the Orwell Glacier moraines and Port Jebsen moraines the colonization of rock by *U. antarctica* was apparently prior to that by *R. geographicum.*

TABLE I. MEAN ANNUAL GROWTH RATE AND PRODUCTION OF *Usnea antarctica* AND *U. fasciata* DERIVED FROM THE AGE OF MORAINES DATED BY THE SIZE OF *Rhizocarpon geographicum* THALLI

| *Site and number of moraine* | | *Altitude* (m) | *Approximate age of moraine* (years A.D.) | *Maximum dry weight of thallus* (g) | *Growth rate* (assuming synchronous colonization by *Usnea* and *Rhizocarpon*) (mg year$^{-1}$) | *Production* (mg g$^{-1}$ year$^{-1}$) | *Growth rate** (assuming *Usnea* colonizes before *Rhizocarpon*) (mg year$^{-1}$) |
|---|---|---|---|---|---|---|---|
| *Usnea antarctica* | | | | | | | |
| Moraine Valley | I | 8 | 1514 | 3.64 | 7.91 | 2.17 | |
| | X | 40 | 1424 | 2.59 | 4.70 | 1.82 | |
| | XI | 40 | 1674 | 3.08 | 10.27 | 3.33 | |
| Port Jebsen | I | 130 | 1324 | 2.19 | 3.37 | 1.54 | |
| | II | 130 | 1604 | 1.69 | 4.56 | 2.70 | 1.5 |
| Sombre Lake | I | 8 | 1474 | 2.93 | 5.86 | 2.00 | |
| | II | 15 | 1604 | 2.05 | 5.54 | 2.70 | 5.6 |
| *Usnea fasciata* | | | | | | | |
| Moraine Valley | I | 8 | 1514 | — | — | — | |
| | X | 40 | 1424 | 8.67 | 15.74 | 1.82 | 18.5 |
| | XI | 40 | 1674 | 4.01 | 13.33 | 3.32 | |
| Port Jebsen | I | 130 | 1324 | 5.39 | 8.29 | 1.54 | |
| | II | 130 | 1604 | 6.57 | 17.75 | 2.70 | |

* Data derived from Fig. 6.

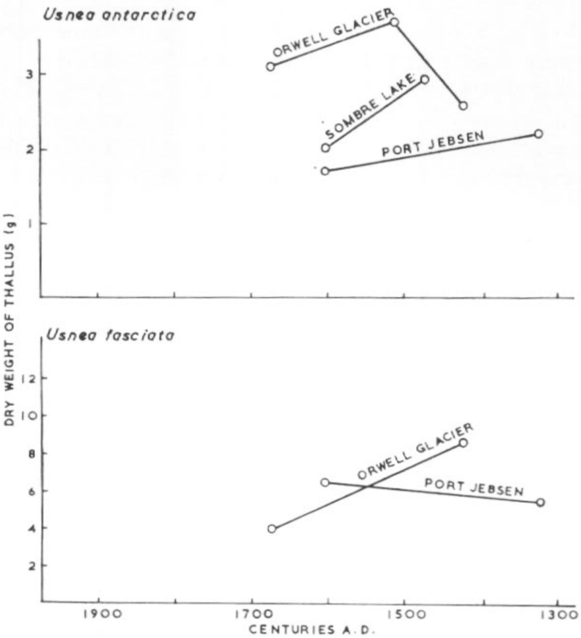



Fig. 6. Ages of thalli of *Usnea antarctica* and *U. fasciata* dated by *Rhizocarpon geographicum* on moraines, demonstrating successional colonization.

The data represented in Fig. 6 also demonstrate the possibility of graphs with negative slopes. This may result either from random colonization without sequence or thallus abrasion (which is shown to be frequent in *Usnea*) has led to weight loss in the oldest specimens. During the spring months on Signy Island, the added weight of melting snow accumulated amongst the thallus frequently causes branches to break. Ice as well as wind abrasion therefore renders these species largely unsuitable for lichenometric treatment. It may be argued that thallus abrasion will only result in the graph slope being flattened (because a large population is being sampled) and that negative slopes result from random colonization, importation of older thalli from adjacent areas (e.g. by rock fall from cliffs) or an historically colder climate retarding the growth rate.

Rates of growth (mg year$^{-1}$) calculated for *U. antarctica* and *U. fasciata* from the graphs (Fig. 6) demonstrate that *U. fasciata* appears to grow up to three times more rapidly than *U. antarctica*, 18.5 mg year$^{-1}$ compared with 5.6 mg year$^{-1}$ (Table I). Furthermore, with *U. antarctica* growth is apparently slower on the Port Jebsen moraines (1.5 mg year$^{-1}$) and this may be due to these moraines being 100 m higher than those at Sombre Lake, and they are also considerably more exposed. On the Sombre Lake moraines, the growth rate calculated for *U. antarctica* (from Fig. 6) is the same as that calculated on the assumption of synchronous colonization with *R. geographicum*, implying that these two species, in reality, did begin to colonize those moraines at the same time (Table I). However, the data for the Port Jebsen moraines indicate a successional colonization with *U. antarctica* becoming established prior to *R. geographicum*. In the absence of more data, these points are difficult to resolve. Graphs with negative slopes have not been used to estimate annual growth rate in this manner, although the data in Table I might be taken to indicate that *U. antarctica* on the Orwell Glacier moraines has a more rapid rate of growth than that recorded on the other two moraines. *U. fasciata* only infrequently occurs below 15 m a.s.l. and thus was not recorded on the Sombre Lake moraines or on the Orwell Glacier moraine I.

Net annual production rates calculated for moraine lichens are noticeably less than the directly measured rates (Figs 3 and 4). However, since thalli studied on the moraines were much larger (and therefore older) than those thalli directly measured, these differences are interpreted as an indication that net annual production may decline with increasing thallus age.

Where productivity has been calculated on the assumption that *Usnea* and *R. geographicum* colonized the moraines synchronously, growth is always more rapid on the younger moraines (Table I), further implying that the lichens may demonstrate a senescent phase of decreasing growth rate. When the net annual production of *U. antarctica* is plotted against the time of moraine colonization by *R. geographicum*, this senescent phase is shown to be non-linear (Fig. 7). If the cause of this observed effect were merely due to thallus abrasion, the graph in Fig. 7 would be expected to be linear. Thus, although this senescent phase is apparently

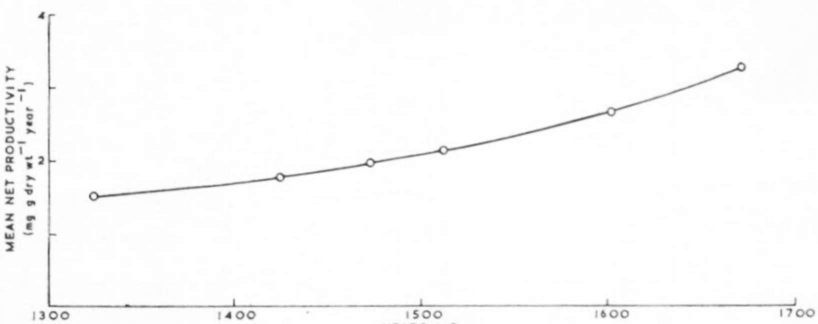



Fig. 7. Senescent net productivity pattern of *Usnea antarctica* on moraines.

biological, the possibility remains that the thallus attains a maximum size (perhaps defined by local habitat factors) and thereafter ceases to grow and is eventually eroded and lost.

*Colonization of timber.* Occasional pieces of timber (pine) around the British Antarctic Survey station on Signy Island (established in 1947) have become weathered into a condition suitable for lichen establishment. Data are recorded from three such timbers in Table II. One of these, part of the fresh-water reservoir, was erected in 1964, and the other two timbers are believed to derive from the original station hut when it was dismantled in 1950.

TABLE II. MEAN ANNUAL GROWTH RATE AND PRODUCTION OF *Usnea antarctica* DERIVED FROM MAXIMUM DRY WEIGHTS OF THALLI GROWING ON PEBBLES IN ABANDONED GIANT PETREL NESTS AND TIMBERS OF APPROXIMATELY KNOWN AGE

| Site | *Age of substratum* (years A.D.) | *Maximum dry weight of thallus* (g) | *Growth rate* (assuming immediate colonization of substratum) (mg year$^{-1}$) | *Production* (assuming immediate colonization of substratum) (mg g$^{-1}$ year$^{-1}$) | *Growth rate* (assuming colonization after 5 year weathering period) (mg year$^{-1}$) | *Production* (assuming colonization after 5 year weathering period) (mg g$^{-1}$ year$^{-1}$) |
|---|---|---|---|---|---|---|
| *Pebbles* | | | | | | |
| 1. Knife Point | 1956 | 0.22 | 11.99 | 55.50 | | |
| 2. Knife Point | 1956 | 0.04 | 2.16 | 55.50 | | |
| 3. Factory Bluffs | 1956 | 0.16 | 8.67 | 55.50 | | |
| 4. Factory Bluffs | 1956 | 0.16 | 8.74 | 55.50 | | |
| 5. Factory Bluffs | 1956 | 0.10 | 5.55 | 55.50 | | |
| 6. Berntsen Point | 1920 (?) | 0.77 | 14.27 | 18.52 | | |
| 7. Berntsen Point | 1920 (?) | 0.78 | 14.39 | 18.51 | | |
| *Timbers* | | | | | | |
| 1. Berntsen Point | 1950 | 0.14 | 5.96 | 41.65 | 7.53 | 52.62 |
| 2. Berntsen Point | 1950 | 0.19 | 8.16 | 41.67 | 10.30 | 52.60 |
| 3. Reservoir, Factory Cove | 1964 | 0.09 | 8.87 | 100.00 | 17.74 | 200.00 |

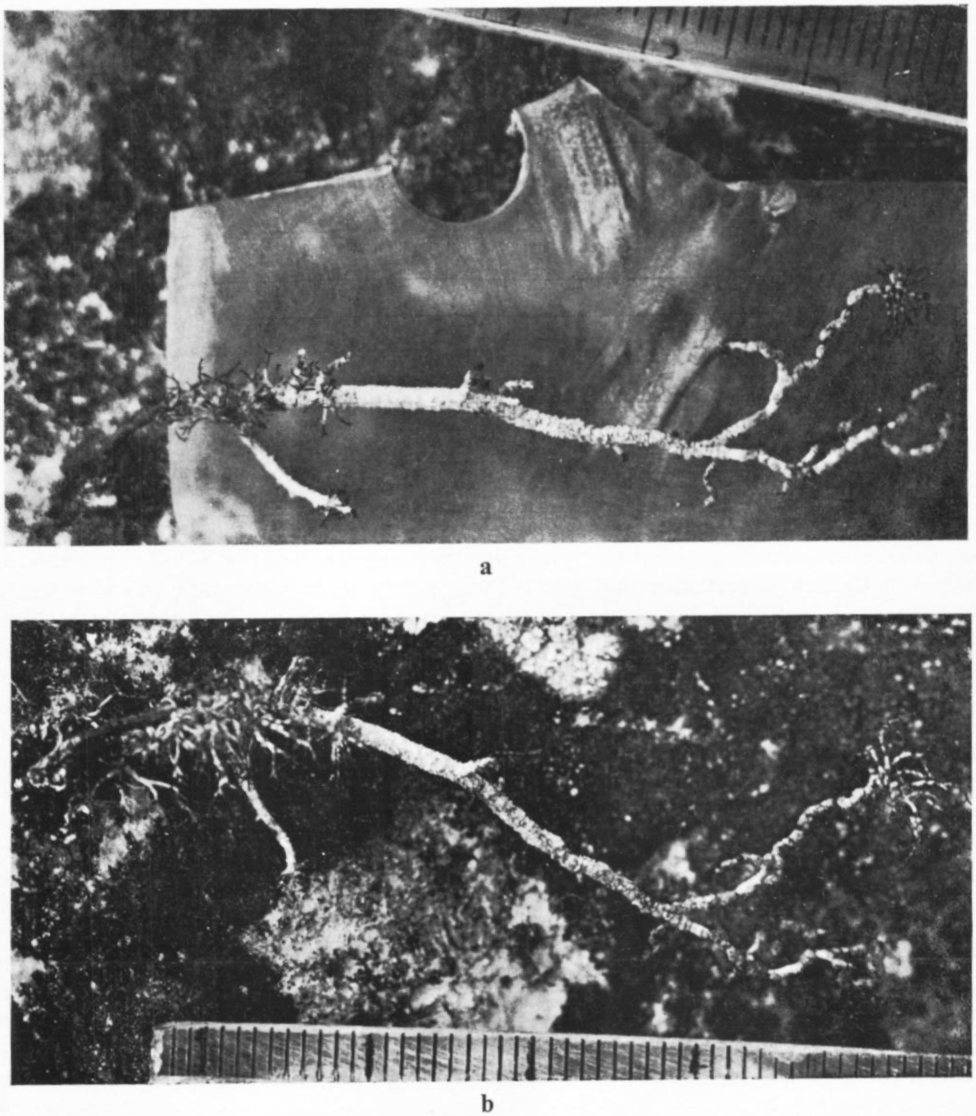
Table II records the maximum dry weights of thalli of *U. antarctica* found on these timbers and their assessed rate of growth assuming immediate colonization. A growth rate has also been calculated assuming an initial 5 year weathering period of the wood. This assumption is based on the field observation that over a 3 year period three-ply wood fibres were weathered into a "hairy" condition that might have been possible to trap lichen propagules, although none was actually observed to do so. The growth rate was estimated to be less than 20 mg year$^{-1}$ and the data are mostly within the range determined for thalli on the moraines (Table I). Because the thalli were young (less than 25 years), their productivity (mg g$^{-1}$ dry weight year$^{-1}$) is high, decreasing with thallus age. Although it is realized that the lichens almost certainly do not colonize the timber immediately, and that a 5 year weathering period is no more than speculative, the net annual production of *U. antarctica* determined on this assumption is in close agreement with that calculated from direct measurements (Fig. 3).

Lindsay (1973) reported finding *U. antarctica* on timbers originating from the derelict whaler's pump house (built *c.* 1920) at Pumphouse Lake on Signy Island in 1967; the maximum dry weight was 63.8 mg, indicating a growth rate of 1.38 mg year$^{-1}$ over *c.* 46 years (i.e. excluding the weathering period). He also recorded a maximum dry weight of 1.1 mg for a thallus growing on timber estimated to have originated from the original British Antarctic Survey station hut (dismantled in 1950), indicating a growth rate of about 0.06 mg year$^{-1}$ over a period of about 17 years. Whereas in the latter case it would now appear that that timber had been more recent than Lindsay estimated, the absence of all lichen growth from the whaler's pump-house timber in 1974 (author's observation) is remarkable,* even if Lindsay

* A few very small thalli of *Usnea antarctica* and of several crustose species were noted in January 1977 by R. I. L. Smith (personal communication).

had removed all the colonized timbers in 1967. It is highly probable that these latter timbers had been treated with creosote, lead paint or similar preservatives that would be toxic to lichen growth.

*Colonization of abandoned giant petrel nests.* Historically, there were small colonies of giant petrels (*Macronectes giganteus*) nesting around Borge Bay, Signy Island. According to various station reports, these nests were numerous on Berntsen Point, Knife Point and Factory Bluffs when the British Antarctic Survey station was established (1947–48), but that by 1955–56 all the nests near the station, or anywhere along the east coast of Signy Island, had been abandoned. The small pebbles comprising these nests are now colonized by *U. antarctica* and



a

b

Fig. 8. Extension growth of branches of *Usnea antarctica* between February 1972 (a) and February 1974 (b).

various crustose lichens. Since it is likely that the pebbles were weathered into a condition suitable for establishment by lichens before the birds abandoned the nests, or even before they were incorporated into the nests, colonization is assumed to have begun almost immediately upon abondonment.

Table II shows the assessed rate of growth of *U. antarctica* on the assumption that colonization began in 1956. Nest 2 demonstrates, however, that colonization may not have been immediate, whilst the large thalli from nests 6 and 7 indicate that those nests had probably been abandoned prior to the establishment of the present station and possibly as early as the 1920's, when whalers occupied the same site. Although little significance should perhaps be attached to these data, the mean rates of growth of *U. antarctica* obtained from different similar substrates at comparable low altitudes compare remarkably, e.g. Knife Point nest pebbles (mean 7.08 mg $year^{-1}$), Factory Bluffs nest pebbles (7.65 mg $year^{-1}$), timber (7.66 mg $year^{-1}$), Moraine Valley moraines (7.63 mg $year^{-1}$), Sombre Lake moraines (5.70 mg $year^{-1}$), and are very similar to the direct growth measurements (8.15 mg $year^{-1}$).

*Linear growth of thallus branches*

Photographic measurements of linear increase of individual branches of *U. antarctica* were not successful. The relative alignment of the branches frequently changed between periods of wetting (when the lichen is totally flaccid) and drying, not only making branch identification difficult but also presenting an orientation that was never perpendicular to the film plane, and therefore gross errors of parallax distortion were encountered. Although it is possible to correct such errors in photographs of radially growing crustose lichens (Hooker and Brown, 1977), these techniques cannot be applied to single branches of fruticose lichens. In only a single thallus, from a total of 70, was it possible to discern any linear increment (in tertiary branches of an old much-abraded thallus (Fig. 8)), amounting to 0.9 mm over a 2 year period (February 1972–February 1974).

Thalli of *U. antarctica* growing on reservoir timber estimated to be 5 years old were 15 mm tall, representing a mean vertical growth rate of 3 mm $year^{-1}$; plants up to 20 mm tall growing on a wooden ramp *c.* 12 years old near the reservoir would have a growth rate of 1.67 mm $year^{-1}$ (personal communication from R. I. L. Smith). Other timbers (Berntsen Point), 19 years old, supported thalli 22 mm tall, indicating a mean growth rate of 1.15 mm $year^{-1}$. Depending on micro-environmental conditions, the lichens apparently have a maximum height, and this "canopy" height of the population is rapidly attained by the young thallus (Fig. 9), whereupon growth is mainly transferred to branching. Although the thallus height is shown to continue increasing slowly, no data are available to suggest that the extension rate of secondary and tertiary branches is also reduced, i.e. growth of branch apices perhaps proceed at a uniform rate (dependent on micro-environmental conditions, until the "canopy" height is attained) throughout the thallus life span.

*Population dynamics*

Fig. 10 shows the size (age) distribution of young thalli of *U. antarctica* growing as a tight continuous stand of plants. It indicates that the proportion of very young thalli is high and that natural juvenile fatality must be a common phenomenon which conceivably may be due to over-crowding and shading effects. *U. antarctica* predominantly reproduces vegetatively (approximately 2% of thalli found on Signy Island were fertile) and large thalli produce very large numbers of soredia. Although habitat factors must weigh heavily against the establishment and survival of every soredium that is produced (the population would be contained by only one successful propagule produced per thallus within its life span of up to at least 600 years) it is surprising to find such heavy losses of juvenile thalli which have successfully become established. Rock surfaces and stones are often densely covered by tiny unbranched *Usnea*

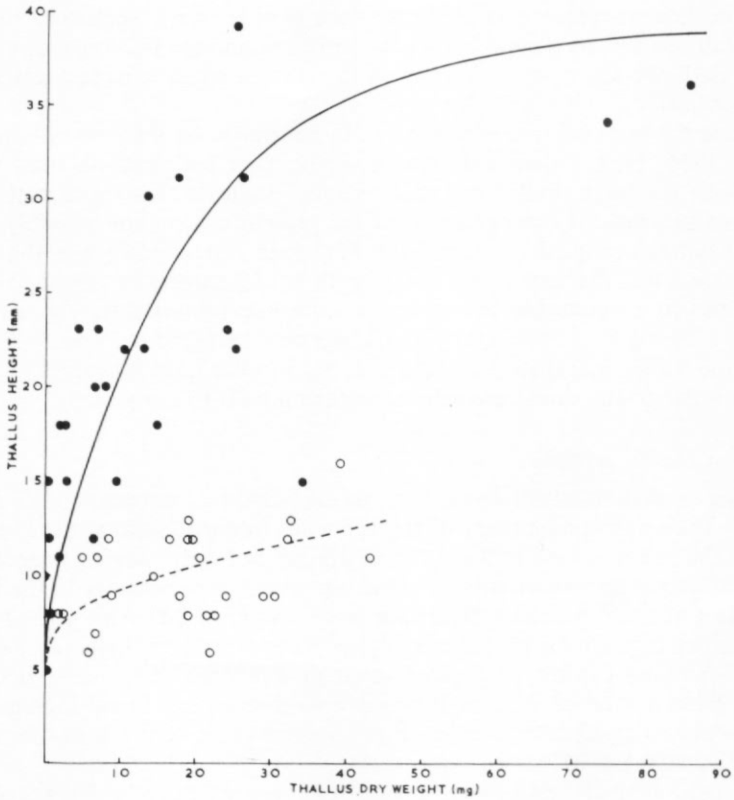



Fig. 9. The effect of micro-environmental conditions on the extension growth of thalli of *Usnea antarctica* on pebbles (●) in abandoned giant petrel nests, and on timbers (○) of the British Antarctic Survey station reservoir.

stems of a few millimetres length. Clearly, therefore, the population size is not defined by successful soredium establishment. Because this latter is excessive, population-controlling factors are apparently exerted on the juvenile thallus within the first 5 years of its life, when the thallus is only a few millimetres tall and may have only a single unbranched stem.

## Discussion

Productivity studies on *Usnea antarctica* and *U. fasciata* by direct measurement proved to be extremely difficult. When dry, the thallus is very brittle and thalli detached from their substratum suffered weight loss by fragmentation. When thalli remained attached to their substratum (pebbles), productivity was erratic, indicating that losses were still occurring (Figs 3 and 4). The dense growth habit of these lichens, particularly *U. antarctica* which frequently forms an almost continuous stand, may be important in reducing abrasion by wind and ice particles.

Direct measurements of *U. antarctica* showed a net annual production of approximately 40 mg $g^{-1}$ dry weight $year^{-1}$ in the mature thallus but production by juvenile thalli (less than 0.5 g dry weight) can be as great as 150 mg $g^{-1}$ dry weight $year^{-1}$. Lichenometrically determined net annual production of juvenile thalli growing on timbers of approximately known age ranged between 50 and 200 mg $g^{-1}$ dry weight $year^{-1}$ in thalli between 0.08 and 0.14 g dry weight (Table II). Lichenometrically determined net annual production in five of seven

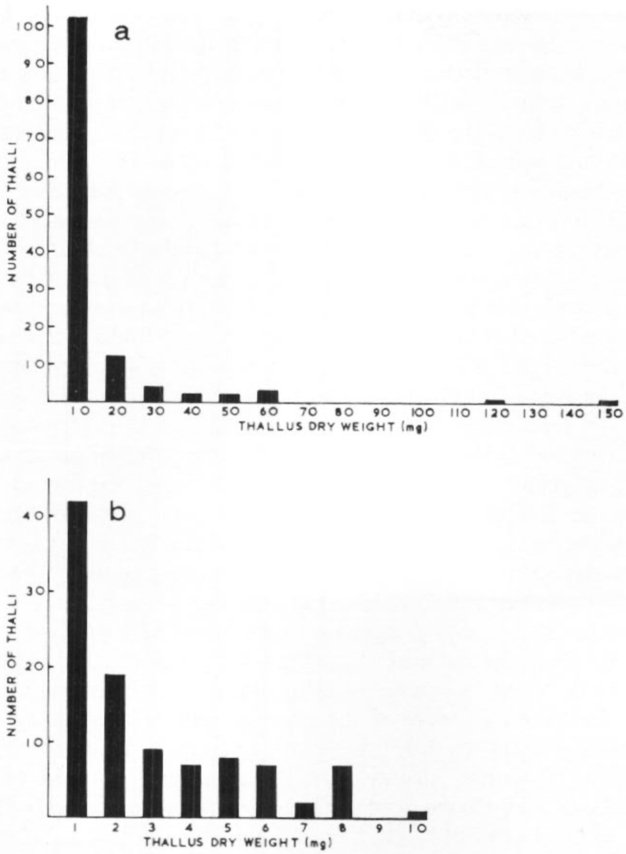



Fig. 10. Size (age) distribution within an area 10 cm² of juvenile thalli of *Usnea antarctica* (a) 0–150 mg dry weight and (b) 0–10 mg dry weight, growing on timber.

abandoned giant petrel nests also agree with these data. In senescent thalli (1–3 g dry weight), the mean net annual production over the whole life span may be as low as 1–5 mg $g^{-1}$ dry weight $year^{-1}$. This latter figure, derived from a lichenometric study of moraines, is tenuous, being based on the assumption that moraine colonization was synchronous with that of *Rhizocarpon geographicum* (a species of known growth rate, viz. 10 mm in diameter $century^{-1}$, whose thalli may be dated). Growth rates (mg $year^{-1}$) accounting for successional colonization have been calculated from the slope of the graphs in Fig. 6 but it is not possible to translate these data into net annual production. However, examination of the data in Table I indicates that the net annual production of senescent thalli (1–3 g dry weight) would be two to three times less than the value of 1–5 mg $g^{-1}$ dry weight $year^{-1}$ quoted above (assuming synchronous colonization with *R. geographicum*). Thus, the data suggest that net annual production decreases with increasing thallus age. In extremely old thalli, aged 300–600 years, the abrasion of thallus branches (as was found from productivity studies involving direct measurement of thalli) will have significantly contributed to reducing the values for net annual production, gross weight loss obviously increasing with time. However, assuming colonization synchrony with *R. geographicum*, the calculated net annual production of senescent thalli of *Usnea antarctica* does not demonstrate a linear decrease with time (Fig. 7) as might be expected if mechanical abrasion were the only factor reducing net annual weight gain. The curved nature of the graph indicates that a biological mechanism associated with ageing results in a continuous decline in the thallus growth rate and also, therefore, in the rate of net annual production.

Studies on the linear growth of thallus branches and identification of meristematic regions was unsuccessful. In only a single thallus out of a total of 70 was it possible to measure growth of tertiary branches arising from the old primary stem of a much-eroded thallus, providing an extension rate of 0.45 mm year$^{-1}$. It is, however, unlikely that this rate will be uniform in all thalli in all habitats. Thalli growing on timber estimated to be between 5 and 19 years old ranged from 15 to 22 mm tall, representing mean growth rates from 3 to 1.15 mm year$^{-1}$. Once the maximum thallus height for a particular micro-habitat is obtained, growth is directed to branching, and the extension rate of the thallus "canopy" height increases slowly (Fig. 9). Were thallus branch growth rate uniform throughout time and in dissimilar habitats, then at the photographically measured growth rate of 0.45 mm year$^{-1}$ thalli 500 years old on moraines could have achieved the length of 22.5 cm. Such thallus sizes were not encountered amongst the stunted cushion-like thalli found on the exposed moraine rocks but were attained by the long pendulous growth forms growing on moist, sheltered northerly rock faces. Lindsay (1976) reported collecting an abnormal specimen of *U. antarctica* 67 cm in length in the South Shetland Islands and suggested a possible age of *c.* 2 230 years. Unfortunately, the specimen was lost in transit to the UK and examination has not been possible. Since an age of even 1 675 years (based on the measured 0.45 mm year$^{-1}$ on Signy Island) is unlikely, Lindsay's specimen further indicates variation in extension rate according to micro-habitat, similar to the growth variation shown between micro-habitats in crustose Antarctic lichens (Hooker, 1980*a*).

*Usnea antarctica* also commonly occurs on moss banks (*Chorisodontium aciphyllum* and *Polytrichum alpestre*) on Signy Island and it had been supposed that this must be an indication of rapid extension growth of the lichen in order to maintain its position on the surface of the turf-forming mosses. However, in view of the photographically recorded extension rate (on rock), together with productivity studies, these loosely attached plants occurring on mosses are considered to occupy a "floating" situation in the manner described for the muscicolous fruticose lichens *Cladonia rangiferina* and *Sphaerophorus globosus* (Hooker, 1980*b*). Even though the moss turves may present a warmer and moister micro-environment than exposed rocks, it is most unlikely that branches of the mature thallus which have achieved canopy height could grow at the required rates of 3–7 mm year$^{-1}$ of the mosses (Collins, 1977) and maintain its position by growth, even though the branches of the lichens have been traced downwards into the turf to a depth of 30–40 mm.

Photographic studies of specimens of *U. antarctica* revealed total thallus loss (by wind) of five out of ten specimens within 4 weeks. Since the whole population on mosses does not decrease as rapidly as this, it is suggested that thalli are continuously mobile on the mosses (removed during gales and "re-anchored" amongst the looser moss shoots which during the following few years' growth will stabilize the lichen), with rate of loss being balanced by rate of input by thalli becoming detached from rock substrata. Juvenile thalli (single branches) are not found between actively growing moss shoots but they have been observed on lichen-encrusted moss surfaces (personal communication from R. I. L. Smith). Occasionally, a moss bank may become heavily colonized with *U. antarctica* but these banks are probably growing at less than 3 mm year$^{-1}$ and the dense coverage of *Usnea* may have further reduced the growth rate of the moss. Generally, therefore, mosses are suggested as being an atypical substratum for *Usnea* on Signy Island and, although the lichens remain photosynthetically active (Hooker, 1977), they have an abbreviated life span, either being blown away in the more exposed situations or enveloped by the more rapidly growing turf-forming mosses.

## Acknowledgements

I am indebted to Dr R. I. L. Smith for supervising field studies; to Drs Smith and D. H. Brown (Department of Botany, University of Bristol) for valuable comments during the preparation of the manuscript; and to Professor D. C. Smith for facilities provided in the Department of Botany, University of Bristol.

*MS received 15 December 1978*

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