FACTORS AFFECTING THE GROWTH OF ANTARCTIC CRUSTOSE LICHENS

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ABSTRACT. The growth of Antarctic crustose lichens was studied over a 5 year period on Signy Island, South Orkney Islands. Growth rate is shown to be extremely variable within the individual thallus and also between thalli in the same micro-environments, and this limited the resolution of differences in growth rate between dissimilar habitats. Within the large variation encountered, it appears that thalli of many species reach a mature rate of growth by the time they are 10 mm in diameter and, although there is some evidence that growth rate continues to increase with thallus age at a very slow rate, the data for this are mostly statistically not significant.

There was a clearly defined seasonal pattern of growth with growth ceasing during the winter, presumably due to the low temperature. Resumption of growth in the spring was apparently hindered by loss of respirable substrate during the winter, coupled with recovery from desiccation effects associated with freezing stresses. Maximum growth was attained in January and February.

Habitat aspect was the most influential environmental variable affecting lichen growth, because it governed the extent of habitat illumination, temperature fluctuation and moisture availability. Significant differences in growth rate between some of the sites studied were directly attributable to substratum aspect and its effect on water availability. Growth response to nutrient enrichment was shown by *Caloplaca* cf. *cinericola*.

THE extreme longevity and slow growth rate of most species of crustose lichens have hindered studies on these plants such that the patterns of productivity and factors affecting the growth rate are only partially understood. There has been difficulty in finding suitably accurate methods of measuring small growth changes in thallus size. Even when the methods of separate studies are clearly stated, the data are not always comparable because growth has been expressed in terms of increased diameter and area (Hale, 1974), the latter sometimes being described as a percentage increase (Rydzak, 1961) or used in computation of relative growth rate (Woolhouse, 1968; Armstrong, 1974). Because of the methodological difficulties, several early studies were confined to only a few individual specimens (e.g. Hausman, 1948), taking no account of variation of growth rate within thalli or between different habitats.

Variation in annual growth rate has been reported by Phillips (1963, 1969), Brodo (1965) and Hakulinen (1966). Rydzak (1961) and Phillips (1963) have reported differences between summer and winter growth rates, and Hale (1970, 1974) and Armstrong (1973) were able to demonstrate monthly differences in growth rate. Hale (1959), Rydzak (1961), Armstrong (1974) and Proctor (1977) have studied the effect of the thallus age on lichen growth rate.

The relative importance of various environmental parameters and their effect on the growth rate of lichens is incompletely understood. The difficulty of accurately measuring thallus size in the field has precluded the study of sufficiently large numbers of specimens for statistical analysis. Although some information is available for non-crustose lichens on the importance of light, temperature and moisture, e.g. Brodo (1965), Lange and Bertsch (1965), Hakulinen (1966), Hale (1970), Kärenlampi (1971), Kershaw and Rouse (1971) and Armstrong (1975, 1976a, 1977), the data on crustose lichens are limited to those reported by Armstrong (1973).

Previous growth studies of crustose lichens in polar regions have been related to lichenometric dating of geomorphological features, e.g. Andrews and Webber (1964), Beschel (1965), Miller and Andrews (1972), Denton and Karlen (1973), Foyer (1973) and TenBrink (1973), and growth curves have been indirectly established by assessing growth rates from dated substrata. Within the maritime Antarctic, TenBrink and Curl (1973) used lichenometric techniques to date raised beaches in the South Shetland Islands but, without measuring growth rates, they were only able to base their studies on relative growth rates. Lindsay (1973) produced a growth curve for two Antarctic species (*Caloplaca* cf. *cinericola* and *Usnea*

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antarctica) on Signy Island, South Orkney Islands, by comparing thalli sizes on recent substrata of approximately known age and these data have been used by Curl and TenBrink (1974) for further lichenometric dating of glacial chronology in the South Shetland Islands.

The aim of this paper is to demonstrate the variation of radial growth rate within individual thalli of crustose saxicolous lichens, and to consider the determining influence of the environment upon crustose lichen productivity in the Antarctic. The study was carried out on Signy Island, South Orkney Islands, between February 1972 and April 1974. A number of quadrats was established for long-term studies and individual thalli of several species were photographed at intervals of 2–3 years. Additional information has been derived from photographs taken in February 1977 and this is incorporated in the present paper.

The South Orkney Islands lie in the maritime Antarctic zone (Holdgate, 1964, 1977) in the southern part of the Scotia Ridge on the northern limit of the Weddell Sea. Signy Island (lat. 60°43′S, long. 45°38′W) is a small island of about 40 km² with a small permanent ice cap and a maximum altitude of 279 m a.s.l. In the summer months much of the coastal low-lying ground is free of snow and ice (Holdgate, 1967; Collins and others, 1975). The topography of the island is rugged with unstable glacial debris and immature soils (Chambers, 1966; Matthews and Maling, 1967) but there exists, however, a relatively rich cryptogamic flora and a wide range of moss- and lichen-dominated communities associated with a variety of different habitats (Holdgate, 1964; Longton, 1967; Smith, 1972), which are locally subject to an extreme biotic influence of large populations of seals, penguins and small petrels.

Signy Island's position south of the Antarctic Convergence, particularly in relation to the cold north-east-flowing current of the Weddell Sea, determines a relatively severe climate. During the short summer (late November to late March) the mean monthly temperature for the warmest month (February) rises to 0.9°C and there is usually abundant water available as rain and snow melt, although frost and snowfalls are frequent throughout the summer. However, in winter between May and October, the surrounding frozen sea creates a cold rather arid climate with the mean monthly temperature falling to −10.3°C in July. Total annual precipitation is *c*. 400 mm, much of which occurs as snow. Monthly meteorological data over a 20 year period have been summarized by Smith (1972).

Study Sites

The locations of the sites on Signy Island where crustose lichen growth was studied are shown in Fig. 1. Sites were selected near the coastline (where several were associated with dense penguin rookeries) and also inland on moraines. Details of each site are given in Table I. Site 1 (not shown in Fig. 1) is situated at Shingle Cove, Coronation Island, about 3 km north-north-east of North Point, Signy Island.

Methods

The radial growth rate of crustose lichens was measured from photographs, using correction factors for eliminating errors due to photographic distortion (Hooker and Brown, 1977). 15 species (Table II) were studied at a total of 32 sites of different aspect, slope and degree of nutrient enrichment (Table I). At each site (except that for *Buellia russa*), 5–12 thalli were selected for measurement, with *Xanthoria elegans* being the most intensively studied species. (Although *Xanthoria* is a genus of foliose species, *X. elegans* grows closely attached to the rock substratum, has no distinct lower cortex and is thus considered in this study as a crustose saxicolous lichen.) Specimens from sites 2–7 were measured using the radial photographic distortion correction method (Hooker and Brown, 1977), measuring 8–16 thalline lobes or radii from each thallus. Lichens in sites 1 and 8–15 were measured using the axial photographic distortion correction method (Hooker and Brown, 1977), measuring only four radii on each thallus. This method of measurement has been shown to be accurate to ±0.05 mm.

TABLE I. DETAILS OF STUDY SITES ON SIGNY ISLAND

Site number	Species	Locality	Grid reference*	Aspect	Slope (degrees)	Altitude (m a.s.l.)	Rock type†	Nutrient enrichment status‡	Sea spray§	Melt water§
1	*Xanthoria elegans* (Link) Th. Fr.	Shingle Cove, Coronation Island	None	Level	0	6	QMS	2	–	–
2	*Xanthoria elegans*	Pageant Point	10455 04290	SE	5	10	QMS	2	–	–
3	*Xanthoria elegans*	Factory Cove	10388 04518	N	5	1	QMS	1	+	–
4	*Xanthoria elegans*	Lenton Point	10354 04283	N	80	2	QMS	1	+	+
5	*Xanthoria elegans*	Pageant Point	10456 04285	S	90	1	QMS	4	+	+
6	*Xanthoria elegans*	Spindrift Rocks	10148 04795	W	90	2	QS	4	+	+
7	{ *Caloplaca* cf. *cinericola* *Buellia russa* (Hue) Darb.	Knife Point	10370 04530	N	80	20	A	3	–	+
8	*Caloplaca* cf. *cinericola*	Moraine Valley	10317 04525	N	80	20	QMS	1	–	–
9	*Caloplaca* cf. *cinericola*	Tern Cove	10355 04766	N	90	20	QMS	0	–	+
10	{ *Caloplaca cirrochrooides* (Vain.) Zahlbr. *Buellia russa* (Hue) Darb.	Berntsen Point	10412 04549	N	80	2	S	1	+	+
11	*Caloplaca cirrochrooides*	Berntsen Point	10413 04548	E	5	1	QMS	0	+	–
12	*Caloplaca cirrochrooides*	Berntsen Point	10414 04547	NE	45	1	HMS	0	+	–
13	*Buellia latemarginata* Darb.	Factory Cove	10388 04518	NW	45	1	S	1	+	–
14	*Buellia latemarginata*	Pageant Point	10462 04290	Level	0	20	MS	2	–	–
15	*Acarospora macrocyclos* Vain.	Pageant Point	10447 04287	Level	0	4	MS	5	–	+
16	*Haematomma erythromma* (Nyl.) Zahlbr.	Pageant Point	10456 04291	W	90	20	QMS	4	–	+
17	*Haematomma erythromma*	Factory Cove	10388 04518	SW	45	1	QMS	1	+	–
18	*Rhizocarpon geographicum* (L.) DC.	Factory Cove	10370 04508	S	90	50	QMS	0	–	+
19	*Rhizocarpon geographicum*	Moraine Valley	10305 04468	Level	0	35	QMS	2	–	–
20	*Rhizocarpon geographicum*	Moraine Valley	10305 04468	E	90	35	QMS	0	–	–
21	*Rhizocarpon geographicum*	Moraine Valley	10318 04520	E	80	8	QMS	1	–	–
22	*Rhizocarpon geographicum*	Moraine Valley	10318 04520	N	80	8	QMS	1	–	–
23	*Rhizocarpon geographicum*	Moraine Valley	10318 04520	W	45	8	QMS	1	–	–
24	*Rhizocarpon geographicum*	Tern Cove	10366 04758	W	90	30	QMS	0	–	–
25	*Buellia* sp. A	Factory Cove	10370 04508	S	90	50	QMS	0	–	+
26	*Buellia* sp. B	Moraine Valley	10305 04468	S	90	35	QMS	0	–	–
27	*Lecidea* sp. A	Moraine Valley	10307 04463	Level	0	30	QMS	0	–	–
28	*Lecidea* sp. B	Moraine Valley	10305 04470	W	90	35	QMS	0	–	–
29	*Lecidea* sp. C	Moraine Valley	10305 04465	E	90	35	QMS	1	–	–
30	*Lecidea* sp. D	Moraine Valley	10305 04470	E	90	35	QMS	0	–	–
31	*Lecidea* sp. C	Lenton Point	10361 04290	SW	110	4	QMS	3	–	+
32	*Verrucaria ceuthocarpa* Wahlenb.	Berntsen Point	10413 04548	E	5	1	QMS	0	+	–

* From D.O.S. 210, 2nd edition, Signy Island, 1 : 10 000 with 1 km grid, 1975.
† A   Amphibolite; S   Schist; MS   Mica-schist; QS   Quartz-schist; HMS   Hornblende-mica-schist; QMS   Quartz-mica-schist.
‡ 0   No enrichment; 1   Infrequent bird perching; 2   Frequent bird perching; 3   Peat-bank drainage; 4   Guano drainage; 5   Guano drainage and penguins directly.
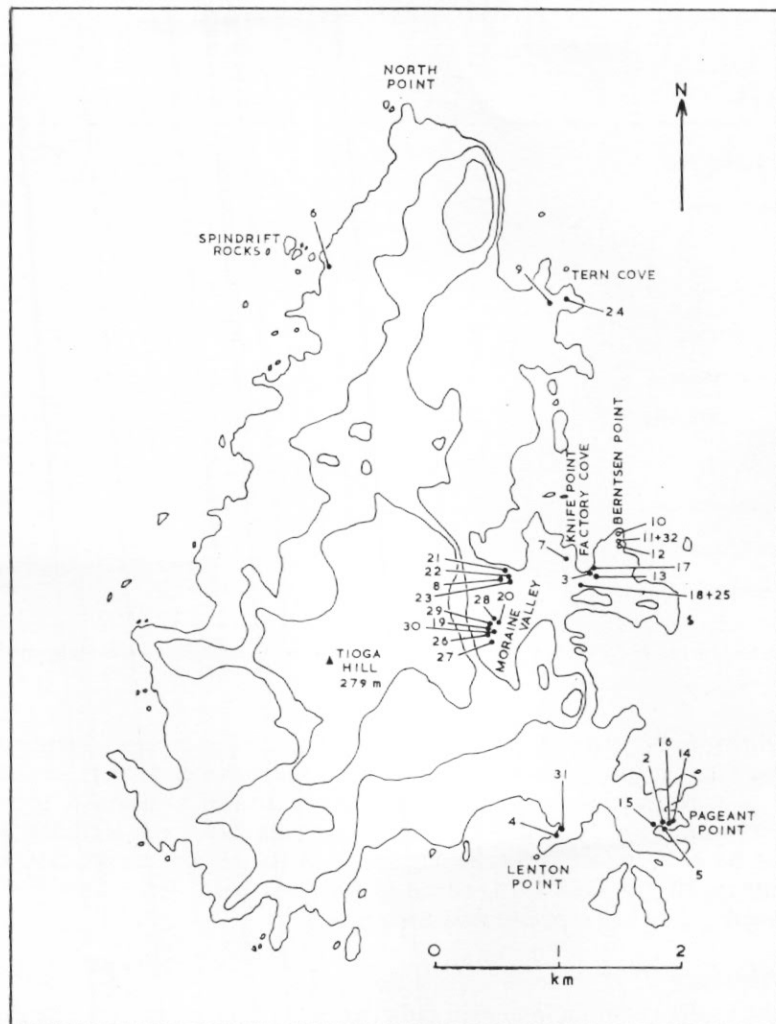§ +   Periodic wetting; –   No wetting.

Fig. 1. Map of Signy Island, showing the location of study sites. The form lines are at 100 m intervals.

Specimens were photographed monthly when dry and when weather conditions were suitable. During the summer months frequent rain restricted periods when thalli were dry, and wet thalli were generally not suitable for measuring because of slight swelling of the thallus. During the winter months, sites which were snow-covered were left undisturbed. At the time of sampling, air, rock and lichen temperatures were recorded using Grant hypodermic thermistor probes. Relative humidity at the lichen surface was recorded with an aspirated Assman psychrometer.

RESULTS

The growth of 294 individual thalli was determined from a total of 2 000 photographs. Of the 15 species studied, *Rhizocarpon geographicum*, *Haematomma erythromma*, the four unidentified species of *Lecidea** and two unidentified species of *Buellia** showed no measurable

* The u nidentified species of *Buellia* and *Lecidea* do not compare with any listed species for Antarctic regions by Filson (1966), Lamb (1968), Lindsay (1971) or Dodge (1973).

TABLE II. NUMBERS OF THALLI STUDIED, RADII MEASURED AND SITES OF EACH SPECIES STUDIED

Species	Number of thalli	Number of radii	Number of sites
Acarospora macrocyclos	10	40	1
Buellia latemarginata	22	88	2
Buellia russa	2	16	2
Buellia spp. (2)	30	*	2
Caloplaca cf. cinericola	31	210	3
Caloplaca cirrochrooides	34	136	3
Haematomma erythromma	18	*	2
Lecidea spp. (4)	28	*	5
Rhizocarpon geographicum	63	*	7
Verrucaria ceuthocarpa	5	*	1
Xanthoria elegans	51	539	6

* Detailed inspection of photographs showed no visible growth throughout the study period (1972–74).

growth over a period of 2 years (1972–74), and *Verrucaria ceuthocarpa* produced no measurable growth during the single growing season when measurements were made (1973–74). Photography of these species in 1977, however, demonstrated measurable growth over the 4–5 year period in most of the study sites and these data have been included in this paper. Measurements have, therefore, been largely confined to the six species (150 thalli) which grew relatively rapidly at sites 1–15, where growth has been determined from a total of 1 029 radii, involving 14 610 separate measurements.

Variation in radial growth rate

Table III shows the variation in annual radial growth of the six species extensively studied. For the thalli of *Xanthoria elegans* (sites 2–5) and *Caloplaca* cf. *cinericola* (site 7), there was some degree of variation in the growth rate between the 2 years (1972–73) and (1973–74). This was statistically significant (*t* test, $P = 0.02$) only for *X. elegans* at site 2 and may perhaps be correlated with the 1973–74 summer having been warmer than that in 1972–73 (Table IV).

Further measurements in 1977 (February) showed that the mean annual growth rate for the years 1974–75 to 1976–77 was twice that recorded for 1972–73 and 1973–74 in *X. elegans* (site 6) and *Buellia latemarginata* (site 13), and 3–4 times greater in *Acarospora macrocyclos* (site 15). No comparable increase was shown by *Caloplaca cirrochrooides* (site 11, Table III). Clearly, there may be considerable variation in performance in different years. Attempts have been made to correlate this increased growth rate with climatological data (Table IV). There is greatest growth correlation with warm summer temperatures in February. Although January and March 1974 had above-average temperatures, this did not appear to stimulate a greater rate of growth than in 1972–73 in *X. elegans* (sites 3–6) or in *Caloplaca* cf. *cinericola* (site 7). Furthermore, January and March in 1975 and 1976 were cooler than in 1974 even though growth rates in the latter 2 years were enhanced. Total monthly precipitation and sunshine (January–March) had no significant effect on the annual growth rate during the

TABLE III. VARIATION IN ANNUAL RADIAL GROWTH RATE OF 12 SPECIES OF CRUSTOSE LICHENS

Species	Site number	Number of thalli measured	Radial growth (mm)										
			1972–73			1973–74			Mean (2 years)	1974–77			Mean (4 or 5 years)
			Max.	Min.	Mean (±S.E.)	Max.	Min.	Mean (±S.E.)		Max.	Min.	Mean	
Xanthoria elegans	1	10				0.39	0.09	0.21 (0.031)					
Xanthoria elegans	2	10	0.31	0.13	0.23 (0.021)	0.45	0.22	0.31 (0.028)	0.27				
Xanthoria elegans	3	8	0.48	0.24	0.41 (0.049)	0.48	0.21	0.36 (0.047)	0.38				
Xanthoria elegans	4	8	0.28	0.11	0.19 (0.038)	0.31	0.09	0.16 (0.026)	0.17				
Xanthoria elegans	5	5	0.48	0.06	0.35 (0.079)	0.54	0.07	0.30 (0.076)	0.32				
Xanthoria elegans	6	10 (4 in 1977)				0.44	0.15	0.28 (0.028)		0.70	0.53	0.59	0.50
Caloplaca cf. cinericola	7	11	0.25	0.11	0.17 (0.015)	0.32	0.10	0.19 (0.025)	0.18				
Caloplaca cf. cinericola	8	8				0.27	0.01	0.13 (0.033)					
Caloplaca cf. cinericola	9	7				0.05	0.00	0.03 (0.018)					
Caloplaca cirrochrooides	10	12				0.12	0.04	0.07 (0.045)					
Caloplaca cirrochrooides	11	9 (3 in 1977)				0.21	0.07	0.14 (0.016)		0.23	0.10	0.18	0.17
Caloplaca cirrochrooides	12	9				0.27	0.04	0.17 (0.021)					
Buellia latemarginata	13	9 (7 in 1977)				0.41	0.13	0.25 (0.029)		0.80	0.31	0.57	0.49
Buellia latemarginata	14	9				0.25	0.04	0.16 (0.027)					
Acarospora macrocyclos	15	7 (3 in 1977)				0.40	0.24	0.33 (0.022)		1.52	0.92	1.30	1.20
Buellia russa	7	1			0.21			0.51	0.36				
Buellia russa	10	1						0.12					
Haematomma erythromma	17	5								0.32	0.10	0.21	
Rhizocarpon geographicum	18	10 (1972–77)									0.00	0.02*	
Rhizocarpon geographicum	21	4 (1973–77)								0.10	0.00	0.06	
Rhizocarpon geographicum	22	7 (1973–77)								0.12	0.00	0.04	
Lecidea sp. B	28	3 (1973–77)								0.10	0.05	0.08	
Lecidea sp. C	29	2 (1973–77)									0.00	0.02*	
Lecidea sp. D	30	3 (1973–77)								0.20	0.10	0.15	
Verrucaria ceuthocarpa	32	3								0.31	0.00	0.18	

*Estimated value determined from the known photographic resolution of 0.1 mm.

TABLE IV. MEAN DAILY AND EXTREME CLIMATOLOGICAL DATA FOR SUMMER (JANUARY–MARCH) AND WINTER (JUNE–AUGUST) MONTHS, SIGNY ISLAND, 1971–77

	1971	1972	1973	1974	1975	1976	1977
Temperature (°C)							
January	1.6	0.3	−0.5	1.5	0.8	1.4	1.7
February	1.2	0.1	1.0	1.5	1.6	2.7	1.6
March	0.7	−0.2	0.6	2.0	−0.5	0.7	0.6
Mean	1.17	0.07	0.37	1.67	0.63	1.2	1.3
Highest maximum	10.3	7.0	10.4	16.2	11.9	10.7	10.6
Lowest minimum	−6.7	−9.4	−6.8	−3.1	−6.6	−5.5	−6.0
June	−5.6	−13.1	−13.0	−9.7	−15.0	−9.2	−3.3
July	−9.4	−9.4	−9.8	−9.3	−13.2	−10.7	−9.4
August	−6.1	−14.9	−8.3	−12.2	−13.2	−9.2	−7.9
Mean	−7.03	−12.46	−10.36	−10.40	−13.80	−10.17	−6.87
Highest maximum	6.1	3.6	6.7	6.2	3.8	5.0	8.2
Lowest minimum	−27.3	−39.3	−30.4	−30.7	−30.8	−27.2	−30.0
Precipitation (*as equivalent rainfall*) (mm)							
January	id	22	117	58	49	13	50
February	id	68	55	83	46	38	47
March	id	12	88	42	29	40	32
TOTAL	—	102	260	183	124	91	129
Sunshine (h)							
January	133.4	65.4	49.6	46.3	38.2	64.6	55.6
February	60.5	37.5	82.5	23.8	37.1	36.0	45.0
March	35.8	19.0	16.4	62.0	25.5	28.4	33.0
TOTAL	229.7	121.9	148.5	132.1	100.8	129.0	133.6

id Insufficient data.
Data from Limbert and Loan (1976*a*, *b*), Limbert (1977*a*, *b*, 1979) and unpublished data.

studied period, and the severity of the 1972 winter did not, apparently, cause any reduction in growth rate in the following summer (1972–73).

In comparing maximum and minimum annual growth rates of thalli measured at each site (1972–73 and 1973–74; Table III), it is evident that there is considerable variation in performance of individual thalli, and this variation is further demonstrated within individual thalli (Table V), a phenomenon which inevitably leads to thalli with irregularly orbicular margins. Variation in growth rate of individual thalline lobes of *Xanthoria elegans* and *Acarospora macrocyclos* may lead to engulfment of lobes that grow relatively more slowly (Hooker, in press).

Comparison of growth rate with thallus size has not been possible in all the sites studied,

TABLE V. VARIATION IN ANNUAL RADIAL GROWTH RATE WITHIN INDIVIDUAL THALLI OF FIVE SPECIES OF CRUSTOSE LICHEN

| Species | Thallus | Increase in radial growth (mm) | | | |
		Max.	Min.	Mean	Max. deviation
Acarospora macrocyclos (site 15)	1	0.55	0.22	0.350	0.200+++
	2	0.49	0.25	0.355	0.135++
	3	0.31	0.22	0.262	0.048
	4	0.32	0.19	0.240	0.080
Buellia latemarginata (Site 13)	1	0.51	0.35	0.410	0.100
	2	0.34	0.23	0.282	0.058
	3	0.45	0.00	0.222	0.228+++
	4	0.27	0.10	0.197	0.097++
Caloplaca cf. *cinericola* (site 8)	1	0.32	0.00	0.160	0.160+++
	2	0.37	0.00	0.220	0.220+++
	3	0.11	0.09	0.100	0.010
	4	0.32	0.21	0.267	0.057
Caloplaca cirrochrooides (site 12)	1	0.32	0.22	0.275	0.055
	2	0.30	0.14	0.207	0.093
	3	0.23	0.06	0.170	0.110++
	4	0.33	0.13	0.185	0.145+
Xanthoria elegans (site 1)	1	0.40	0.16	0.237	0.163+
	2	0.40	0.22	0.342	0.122
	3	0.40	0.15	0.222	0.178+++
	4	0.35	0.16	0.250	0.100

Deviation significant by χ^2 test at: +   10% P.
                                        ++   5% P.
                                        +++ 1% P.

because in some sites thalli were of a similar size. Because of the extreme variation in individual growth rate, large numbers of thalli would have to be measured at each site. Since it was not always possible within a site to find even as many as ten thalli that were suitable for photographic measurement, i.e. as near circular as possible and on flat substrata, the effect of thallus age on growth rate has generally not been demonstrated.

In *Xanthoria elegans*, it appears that the radial rate of growth increased with thallus size and presumably, therefore, with age. This was most noticeable in sites 1, 2, 4 and 5, but calculated correlation coefficients (Fig. 2) are not statistically significant. This pattern was also seen in *Caloplaca* cf. *cinericola* (Fig. 3) and *Caloplaca cirrochrooides* (Fig. 4), but the regression coefficients are significant ($P = 0.05$) only for the former species at site 7 (1972–73). The range of variation in *Acarospora macrocyclos* and *Buellia latemarginata* completely obscures any effect of age on the growth rate in those species (Fig. 5).
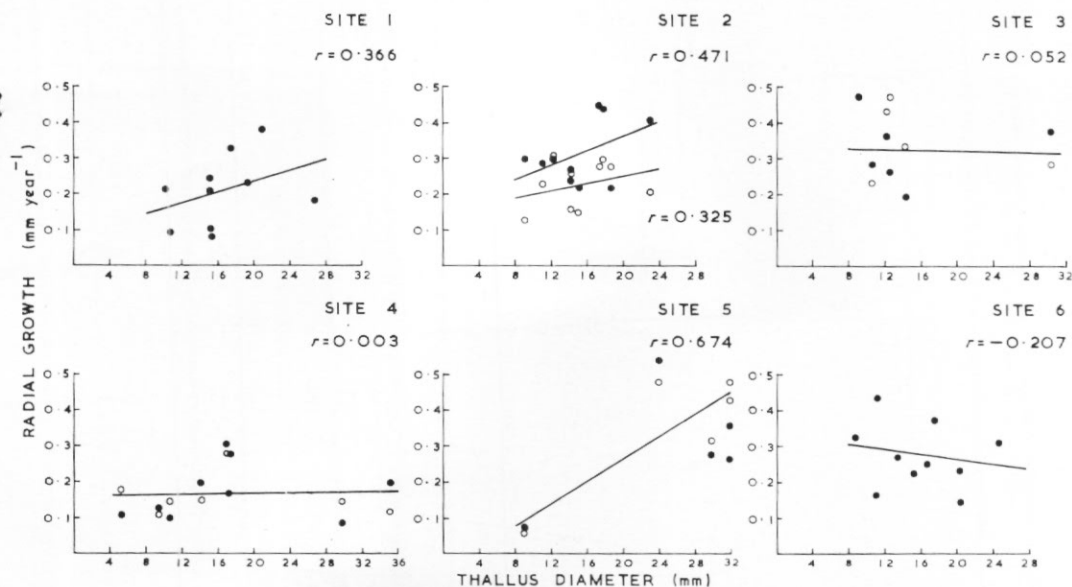
Fig. 2. Radial growth of *Xanthoria elegans*. ○ 1972–73; ● 1973–74.

Seasonal variation in growth rate within species

Antarctic crustose lichens exhibit a distinct variation in monthly growth rate. During the winter months metabolism is presumed to be inhibited as the plants are either buried by snow and ice (for up to 9 months) or exposed to very low temperatures (to −40°C at sea-level at Signy Island) in wind-swept snow-free habitats. Fig. 6 (*Xanthoria elegans*) indicates a small amount of growth occurring between May and October, in particular at site 6. However, this increase occurs during the early spring, between September and October, and should not be interpreted as winter growth. Detailed analyses of errors arising in measurement have shown that *X. elegans* (site 2) does not grow during the winter months (Hooker and Brown, 1977). At the relatively low latitude of Signy Island, light is unlikely to be a limiting factor during the winter months, with day length at mid-winter being about 6 h. During the warmer growing seasons, variation in growth rate is evident but it is possible to demonstrate this only in those species which grew relatively rapidly.

The pattern of seasonal growth recorded (Figs 6 and 7) demonstrates that the lichens grow only to a very limited extent during the spring. Between October and November,
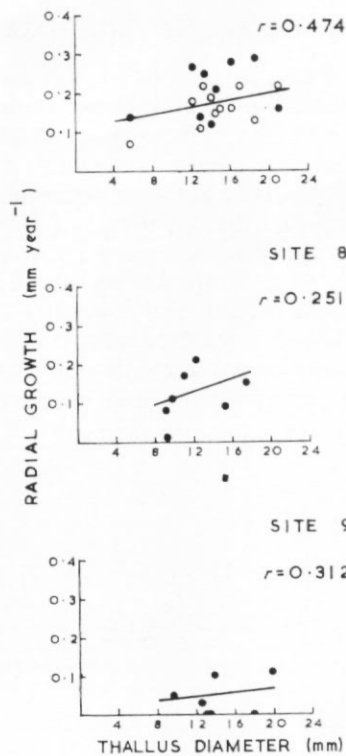
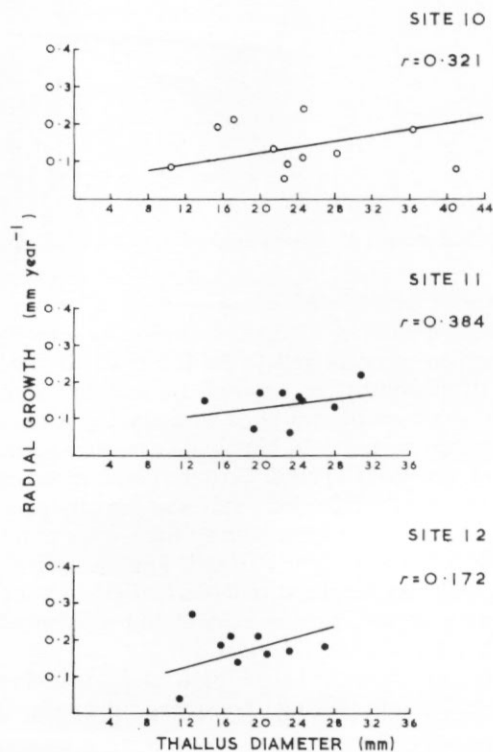Fig. 3. Radial growth of *Caloplaca* cf. *cinericola*. ○ 1972–73; ● 1973–74.

Fig. 4. Radial growth of *Caloplaca cirrochrooides*. ○ January 1973–April 1974; ● January–April 1974.
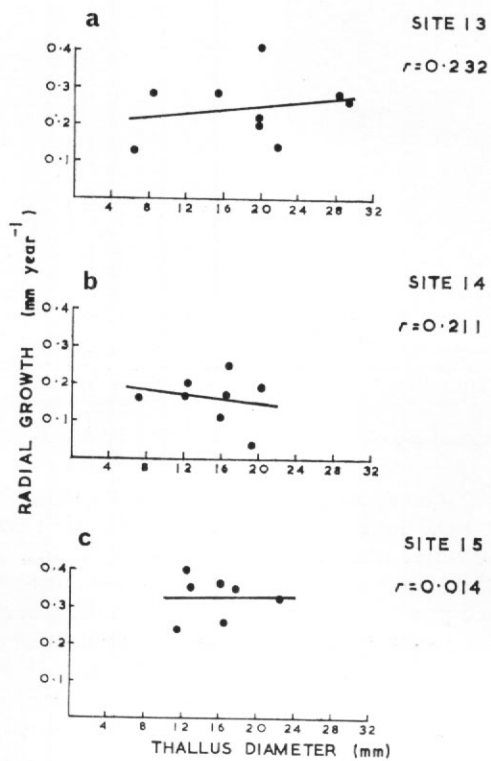
Fig. 5. Radial growth of *Buellia latemarginata* (a and b) and *Acarospora macrocyclos* (c); January–April 1974.
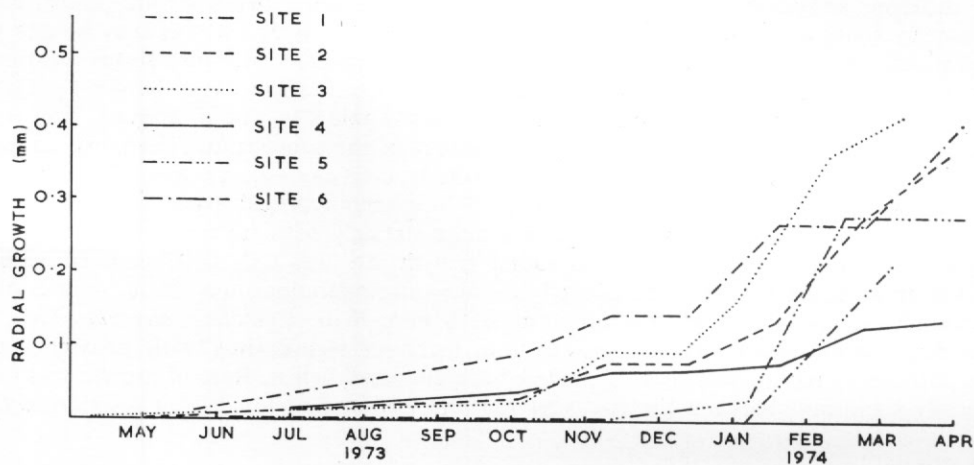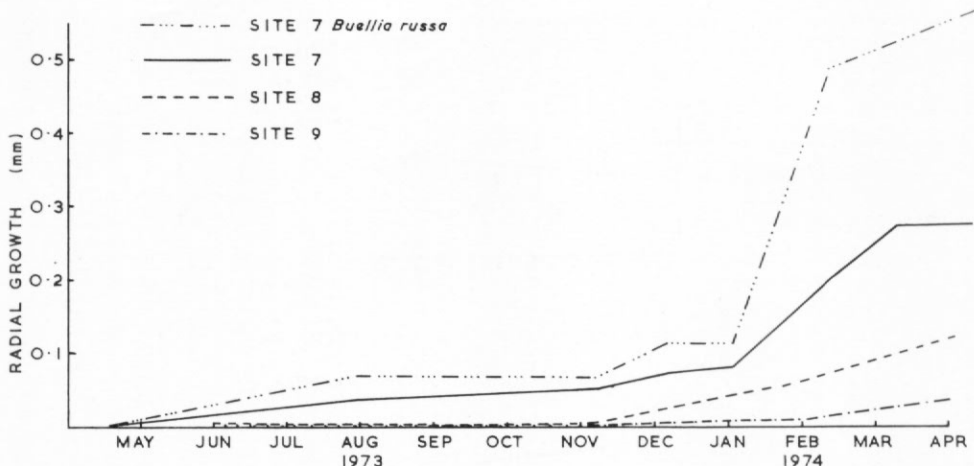

Fig. 6. Seasonal growth of *Xanthoria elegans*.

Fig. 7. Seasonal growth of *Caloplaca* cf. *cinericola* and *Buellia russa*.

X. elegans may achieve 0.05 mm radial growth as rising air temperatures provide moisture from melting winter snow and there is a release of nutrients, particularly nitrogen, from soil and rock surfaces (Northover and Allen, 1967). However, this melt period seldom lasts more than 4–6 weeks and the main period of growth begins in January when air temperatures are frequently above 0°C and precipitation is usually as rain. Between January and February, radial growth may be as much as 0.25 mm and a single thallus of *Buellia russa* (site 7, Fig. 7) radially grew 0.35 mm during this time. After February the growth rate begins to slow again as air temperatures fall, and by April–May all growth has ceased. It is assumed that this pattern also exists, but on a much reduced scale, in very slowly growing species, e.g. *Rhizocarpon geographicum*. Studies on *Acarospora macrocyclos* and *Buellia latemarginata* were initiated late in the 1973–74 season and data on spring growth are absent.

Environmental effect on growth rate

The differing annual rates of growth for *Xanthoria elegans* (sites 1–6) are statistically significant by analysis of variance ($F = 2.79$, $df = 5; 42$, $P = 0.5$) and this may be due to differences in substratum aspect, slope, illumination, temperature, moisture status, nutrient supply and winter snow-cover. The probability levels of significance (t test) between growth rates at different sites were determined for each species (Table VI). For *X. elegans*, inter-site differences of growth rate correlate mainly with aspect of the substratum. The mean annual radial growth rate was 0.38 mm at site 4 (northerly, vertical aspect). For *Caloplaca* cf. *cinericola*, the aspects of sites 7–9 were identical (northerly, vertical aspect) and inter-site differences of growth rate appear to correlate most strongly with nutrient availability. At site 9, an exposed rock face, the annual radial growth rate was only 0.03 mm. However, site 7 was enriched by drainage, particularly nitrate and ammonium ions, from moss banks and here the annual radial growth rate was 0.18 mm. With *Caloplaca cirrochrooides*, a characteristic supra-littoral species, growth rate increases significantly with proximity to the sea, although other factors to be considered are discussed below. Rate of growth was not statistically significant between the two sites (13 and 14) studied for *Buellia latemarginata*.

Micro-climate

Table VII lists representative temperature and relative humidity data recorded synchronously at different sites, showing that temperature of the rock and associated lichens is frequently

TABLE VI. VALUES OF THE *t* STATISTIC AND PROBABILITY LEVELS OF SIGNIFICANCE BETWEEN GROWTH RATES OF FOUR CRUSTOSE SPECIES AT DIFFERENT SITES

Xanthoria elegans

	Sites	*t*					
		1	2	3	4	5	6
df	1		2.135+	3.237++	1.185	2.134	1.524
	2	19		1.250	2.041	0.712	0.798
	3	17	17		2.580+	0.184	2.122
	4	17	17	15		1.854	1.633
	5	14	14	12	12		1.292
	6	19	19	17	17	14	

Caloplaca cf. *cinericola*

	Sites	*t*		
		7	8	9
df	7		3.173++	5.393+++
	8	18		2.061
	9	17	14	

Caloplaca cirrochrooides

	Sites	*t*		
		10	11	12
df	10		3.920++	4.784+++
	11	20		1.207
	12	20	17	

Buellia latemarginata

	Sites	*t*	
		13	14
df	13		1.571
	14	17	

Significance at: +   5% P.
++   1% P.
+++ 0.1% P.

TABLE VII. COMPARISON OF MICRO-CLIMATE AT VARIOUS GROWTH STUDY SITES

Date	Parameter measured		Site 2	Site 3	Site 4	Site 5
10 October 1972	Temperature (°C)	air	−8.5	−2.5	−6.0	−7.5
		rock	−2.5*	14.5*	14.5*	−5.0
		lichen	−2.5*	14.5*	12.0*	−5.0
	Relative humidity† (%)		nd	nd	nd	nd
10 November 1972	Temperature (°C)	air	2.5	2.5	1.0	0.0
		rock	9.0*	7.0*	7.0*	6.5*
		lichen	10.0*	7.0*	5.0*	6.5*
	Relative humidity† (%)		nd	nd	nd	nd
13 January 1973	Temperature (°C)	air	−0.5	nd	1.0	−0.5
		rock	3.0	nd	1.0	3.0
		lichen	3.0	nd	1.0	3.0
	Relative humidity† (%)		67.5	nd	67.5	67.5
2 May 1973	Temperature (°C)	air	−11.5	nd	nd	−11.5
		rock	−11.5	nd	nd	−11.5
		lichen	−11.5	nd	nd	−11.5
	Relative humidity† (%)		100.0	nd	nd	100.0
3 October 1973	Temperature (°C)	air	2.0	4.0	3.0	2.5
		rock	3.5	6.5	10.0*	2.5
		lichen	3.5	6.5	10.0*	2.5
	Relative humidity† (%)		78.0	60.0	50.5	77.7
9 November 1973	Temperature (°C)	air	−2.0	nd	−1.0	−2.0
		rock	0.5*	nd	17.5*	0.5*
		lichen	2.0*	nd	17.5*	2.0*
	Relative humidity† (%)		57.0	nd	44.0	48.0
10 December 1973	Temperature (°C)	air	1.0	nd	2.0	1.0
		rock	8.5*	nd	13.0*	7.5*
		lichen	9.0*	nd	13.0*	8.0*
	Relative humidity† (%)		52.7	nd	52.3	71.5
17 January 1974	Temperature (°C)	air	4.0	nd	nd	5.0
		rock	16.0*	nd	nd	5.5
		lichen	16.0*	nd	nd	6.0
	Relative humidity† (%)		55.8	nd	nd	74.0
21 February 1974	Temperature (°C)	air	1.8	nd	1.5	1.8
		rock	3.0	nd	4.5	2.8
		lichen	3.5	nd	4.5	2.8
	Relative humidity† (%)		91.5	nd	76.5	95.0

* Site in direct sunshine but thermistor probe screened.
† At surface of lichen.
nd No data.

widely different from the ambient air temperature. Direct sunshine resulted in raised micro-climatic temperatures. Site 4, for example, demonstrates the influence of site aspect upon micro-environmental conditions. Such habitats with a northerly aspect also demonstrate a reduction in surface relative humidity; thalli were drier at the north-facing site 4 than at the south-facing site 5 and the difference in annual mean radial growth rate of *X. elegans* at these two sites is marked (0.17 mm and 0.32 mm, respectively). Site 6, facing west, presents an intermediate situation (0.28 mm annual radial growth) but the difference in growth rate between sites 4 and 6, and 5 and 6, is not statistically significant (Table VI). Horizontal surfaces, e.g. sites 1, 2 and 3, were not warmed to such a degree as vertical surfaces with a

northerly aspect but here there was less rapid drainage and evaporation rates were also reduced. The statistically significant difference in growth rate recorded between sites 1 and 3 may be due, in the absence of recorded spring growth at site 1, to an underestimate of the true annual growth rate.

Lichenometric assessment of Caloplaca cf. cinericola on concrete

Some information has been obtained on the growth rate of this species growing on concrete of various installations around the British Antarctic Survey station at Factory Cove. Lindsay (1973) measured the maximum diameter of thalli on these substrata of known age and, assuming immediate colonization of the concrete, calculated the growth rate of *C.* cf. *cinericola* to be 0.15 mm radius year^{-1}. Although there is close agreement between this figure and that measured photographically at site 7 (0.18 mm radius year^{-1}), it is emphasized that Lindsay did not know the period of weathering of the concrete required prior to lichen colonization. Table VIII shows the maximum diameter of the lichens in 1967 (Lindsay, 1973)

TABLE VIII. MAXIMUM DIAMETER OF THALLI OF *Caloplaca* cf. *cinericola* ON DATED SUBSTRATA. THE CALCULATED GROWTH RATES ARE COMPARED WITH THAT MEASURED PHOTOGRAPHICALLY ON AMPHIBOLITE AT SITE 7 (SEE TABLE III).

	Maximum diameter of thalli (mm)		Radial growth rate (mm year^{-1})
	1967*	1974	
Whalers' dam, Factory Cove (A.D. 1920)	10	26	1.10
Meteorological tower, Berntsen Point (A.D. 1951)	1	18	1.20
Amphibolite			0.19

* Data from Lindsay (1973).

and again in 1974 (author's data) demonstrating an annual radial growth rate of 1.1–1.2 mm. This relatively high rate of growth on concrete, compared with that on amphibolite (site 7), is correlated with the high concentration of calcium in the concrete.

From these data, it is possible to determine the duration of concrete weathering prior to the lichen colonization by extrapolation of the straight line graph to its origin. For example, the meteorological tower was erected in 1951 and it is calculated that lichen colonization began on the concrete foundation in 1965 following a 14 year period of weathering. On the whalers' dams, a weathering period of 40 years is indicated prior to colonization by this species. These differences may relate to the differing textures and chemical compositions of the concretes used.

DISCUSSION

The effect of age on thallus growth rate

The data presented here demonstrate considerable variation in the growth rate of Antarctic crustose lichens. This variation not only exists between species but within species at different localities and also between individuals at the same locality. Furthermore, radial growth rate may vary considerably around the margin of individual thalli (Table V). Because of this, it was difficult to demonstrate reliably in such slow-growing plants whether or not age had any significant effect on the thallus growth rate. The data for *Xanthoria elegans* (Fig. 2),

Caloplaca cf. *cinericola* (Fig. 3) and *Caloplaca cirrochrooides* (Fig. 4) suggest that growth rate is slightly enhanced with increasing thallus size (age) but this was statistically significant only for *C.* cf. *cinericola* at site 7 in the 1972–73 austral summer.

Armstrong (1974, 1976*b*) has shown that in the lichens *Parmelia conspersa* and *P. glabratula* ssp. *fuliginosa* there is a slow juvenile pre-linear growth rate in thalli less than 1 cm in diameter; this agrees with earlier studies by Phillips (1963) and Hale (1974) on *P. conspersa*. Proctor (1977) has shown the pre-linear growth rate of *Buellia canescens* to occur in thalli less than 5 mm in diameter. In this study, thalli smaller than 4 mm in diameter were not monitored and the pre-linear juvenile growth phase has not been demonstrated. It is assumed that thalli measured in this study were "mature" specimens. Only in *Caloplaca* cf. *cinericola* was a statistically significant increasing growth rate demonstrated in thalli larger than 1 cm in diameter.

Annual and seasonal variation in growth rate

The annual growth rate of *Xanthoria elegans* (sites 2–6) and *Caloplaca* cf. *cinericola* (site 7) is shown to differ in each of the years studied (1972–73 and 1973–74) but there are insufficient data to make reliable correlations between annual growth rate and the climatic variation between those 2 years. It is, however, suggested that the warm Februaries of 1975 and 1976 (Table IV) may have been responsible for the greatly increased annual growth rate between 1974 and 1977. The possible effect of a severe winter (1959) has been correlated with inhibiting growth of *X. elegans* (Hooker, in press).

Variation in monthly growth rate is most strikingly shown by those species which grew relatively rapidly (Figs 6 and 7). The absence of winter growth is due to prolonged snow-cover (up to 9 months) and/or very low temperatures (to −40°C at sea-level on Signy Island). Between late October and late November, air temperatures frequently rise above 0°C and the spring melt releases nutrients bound in the soil and rock surfaces. While many mosses commence rapid growth during this melt period (Longton, 1970), the present work has shown that the lichens are slow to respond to these favourable conditions. Temperatures are unlikely to be limiting because vigorous growth still occurs during the autumn (late February–April) at equivalent temperature regimes. It appears that the low and prolonged winter temperatures, desiccation effects associated with freezing, and possibly the diurnal freeze–thaw cycles in spring may result in cellular damage and a physiological imbalance which delays spring growth (Hooker, 1977). Gannutz (1970) showed that during the winter and early spring there is a critical reduction of respirable substrate in Antarctic lichens that completely inhibits nocturnal respiration during this period.

Lange and Kappen (1972), working with lichens from Victoria Land, Antarctica, reasoned that the major metabolic activity must take place during the spring, in spite of freeze–thaw interruption, because the lichens there are in contact with liquid water only during this period. However, in the northern maritime Antarctic, where summers are relatively warm and frequently wet, maximum thallus growth rates are shown to be achieved during the summer (Figs 6 and 7). It has been noted above that February is probably the period of most significant growth for *Xanthoria elegans*, *Buellia latemarginata* and *Acarospora macrocyclos*, although growth was also comparatively rapid during January.

The seasonal pattern of Antarctic lichen growth (also demonstrated in Antarctic fruticose lichens (Hooker, 1977)) contrasts with that shown in the temperate lichen *Parmelia caperata* (Hale, 1970), in which maximum growth was recorded during the early summer, with a rapidly declining autumnal rate. Armstrong (1973) demonstrated that growth roughly paralleled monthly rainfall and in two crustose lichens, *Lecidea tumida* and *Rhizocarpon obscuratum*, growth was greatest during the summer months. Showman (1977), who also studied *Parmelia caperata*, was unable to demonstrate any significant pattern of growth rate in that species over a 3 year period.

The influence of substratum aspect and water availability

Substratum aspect and slope appear to be the dominant factors affecting lichen growth in the Antarctic, because by governing habitat illumination they also control temperature, evaporation and snow settlement, and thus profoundly influence local micro-climate. Environmental variables associated with aspect have been fully discussed by Barkman (1958), who concluded that their influence on moisture conditions may be the most critical factor, as confirmed by Fletcher (1973) and Armstrong (1975, 1976a). Rock slope is important in relation to drainage.

Substratum aspect is of special importance under the low-angled polar sun. South-facing slopes in the Arctic receive considerably more warmth than horizontal surfaces (Wilson, 1957). This effect probably diminishes with increasing latitude when the angle of the sun is permanently low with little variation between midday and midnight. In the South Shetland Islands (lat. 61°S, long. 60°W), Greene and Longton (1970) noted a difference of 11.2°C between north- and south-facing slopes on Deception Island, and that in summer in the maritime Antarctic there are wide and rapid diurnal temperature fluctuations. Differences of 10–20°C commonly exist between plant level and air temperature (Wright, 1975), and this is especially common during periods of direct sunshine (Table VII), and there may even be considerable warming during bright but overcast conditions (Longton and Holdgate, 1967). The effect of temperature on Arctic vegetation has been discussed by Wilson (1957), who also demonstrated that the micro-environmental temperature often has a steep vertical gradient, increasing by as much as 1°C cm⁻¹ towards the vegetation or soil surface.

On Signy Island, rocks with a northerly aspect (sites 4 and 7–10) received direct insolation and on calm sunny days the temperature of the rocks and associated lichens frequently reached 20°C even when the air temperature was below 0°C (Table VII). If, however, the duration of sunshine is prolonged, the lichens will become desiccated to the point of reduced or inhibited metabolic activity, this being reflected in the low rate of growth of *X. elegans* at site 4. Rocks with a southerly aspect may be much cooler but this is balanced by a prolonged retention of surface moisture, often in the form of ice. Thus, although metabolic activity as governed by temperature is reduced in plants with a southerly aspect, the time available for metabolism is longer, and in terms of gross productivity this may be the more favourable situation, as shown by the relatively high rate of radial growth of *X. elegans* (0.32 mm year⁻¹) at site 5 (Table III). Net carbon assimilation for most terricolous lichens is optimal at 60–95% thallus water content (Ried, 1960; Harris, 1971; Kershaw, 1972).

Site aspect may significantly control the frequency of wetting and drying cycles. Lichens suffer carbon loss by cellular leakage and excess respiration when wetted (Smith and Molesworth, 1973; Farrar and Smith, 1976). If the wetting is followed by rapid drying, as may occur on rocks with a northerly aspect, carbon loss might not be re-gained by photosynthesis, whereas wetting followed by slow drying (as on southerly aspects) can produce a faster rate of growth, suggesting that carbon losses are made good before the thallus is dry (Armstrong, 1976a). Although in this study a correlation is shown in *X. elegans* between growth rate and substratum aspect, this is not universal to all lichen species. Armstrong (1977) has shown by transplantation experiments that the radial rate of growth (northern temperate species) in north-westerly compared with south-easterly aspects was increased in *Parmelia glabratula* ssp. *fuliginosa* but declined in *P. conspersa* and *Physcia orbicularis*, and no preferential growth was demonstrated by *Parmelia saxatilis*.

Ahmadjian (1970) and Lamb (1970) considered that the availability of water has a greater influence than temperature on the distribution of Antarctic plant communities. However, Ahmadjian found no clear distributional patterns of rock lichens that could be related to moisture availability or exposure, but Smith (1972) described several examples of lichen communities correlated with each factor.

Greene and Longton (1970) attached importance to temperature with regard to dry-weight

production in Antarctic plants, particularly in relation to snow-cover. Exposure to wind and orientation of the rocks govern the extent of winter snow-cover. Since snow is thermally insulating (Larson and Kershaw, 1975; Wright, 1975), it provides protection against the extremely low, widely and rapidly fluctuating winter temperatures. Wright has shown that snow-cover effectively reduces ground temperature compared with those experienced at the snow/air interface, and that during the early spring (September) on Signy Island air temperatures below 30 cm snow depth are the same as the mean monthly air temperature. At this time of year on Signy Island, temperatures fluctuate between $-25°$ and $5°C$ and may range $25°C$ within a 12 h period. Gannutz (1970) recorded that snow-covered mosses and lichens maintained their temperature above $-6°C$ almost continuously at Palmer Station, Antarctic Peninsula, during the winter months (July–September) when winter air temperatures frequently reach $-25°C$. The degree of winter snow-cover, however, appears to have little effect on lichen growth rate in the present study, where all horizontal sites had at least 15 cm of snow-cover between May and August. Larson and Kershaw (1975) stated that a deep covering of winter snow may even reduce lichen annual productivity. Since the depth of snow relates directly to the rapidity with which the ground is exposed in spring, an exposed locality may have a much longer effective growing season than that found in more sheltered areas.

The effects of nutrients on growth rate

On Signy Island there are large populations of penguins, cliff-breeding petrels and also seals which locally add greatly to the nitrogen and phosphate enrichment of soils (Allen and others, 1967), so that most of the crustose lichen-growth study sites differed in their nutrient status. Drainage from bird guano and black reducing muds of the elephant seal wallows, where nutrient levels may be so high as to be toxic to plants (Allen and others, 1967), raises the nutrient status of adjacent localities, and this is reflected in a localized flora of nitrophilous lichen species. Nutrients, particularly nitrate-nitrogen and phosphate bound in the extensive moss banks of *Polytrichum alpestre* and *Chorisodontium aciphyllum*, are slowly released in melt water during the spring and summer (Northover and Allen, 1967). Input of nutrients in these moss turves is derived from precipitation, wind-blown dust and nesting birds, and during stormy weather marine salts are blown inland and deposited over all the island (Holdgate and others, 1967).

The effect of nutrients on crustose lichen growth is most clearly shown by *Caloplaca* cf. *cinericola* (sites 7–9) where increased growth rate at site 7 is attributed to drainage from extensive moss banks above the site (Table III; Fig. 7). This species shows a preference for calcareous rocks, mainly marble and amphibolite, but also quartz-mica-schists with garnet and hornblende porphyroblasts, and on calcium-rich concrete the radial rate of growth is shown lichenometrically (Table VIII) to be five times greater than recorded photographically on amphibolite (site 7).

In *Xanthoria elegans* (sites 1–6), the effect of nutrients is not clear because of other significant environmental variables dominating, e.g. substratum aspect and moisture availability. Sites 1 and 2 were raised boulders within penguin rookeries but were inaccessible to penguins and guano drainage, whereas sites 5 and 6, also within rookeries, received considerable enrichment (Table II). Although *X. elegans* is an ornithocoprophilous species characteristic of areas of biotic enrichment, differences in growth rate between sites correlate chiefly with site aspect even though nutrients play an important role in determining the distribution of the species. Enhanced growth rate due to nutrient addition has been shown by Hakulinen (1966) for the foliose species *Parmelia centrifuga*, *P. conspersa* and *P. saxatilis*. Jones and Platt (1969) have experimentally confirmed this effect with *P. conspersa* and have shown by controlled experiments that this increase is not due to increased moisture content.

Caloplaca cirrochrooides, a hygrohaline species, was the only lichen studied in relation to sea spray. This species is characteristic of the splash zone, where it forms a distinct orange zone on the rocks. Fletcher (1973) considered species of this supra-littoral zone to have a requirement for sea-spray inundation and that distribution followed a gradient of wetness. Although site 10 was higher up the shore than sites 11 and 12 and the growth rate was less than at the latter two sites, the site was also more arid by virtue of its vertical slope and northerly aspect. Thus, although the importance of moisture is apparent, the effect of marine salts upon the growth rate (demand or tolerance ?) remains obscure.

Longevity

The absence of a statistically significant difference between growth rates determined at many of the sites is attributed to the very small amounts of growth recorded, particularly in species of extreme longevity, e.g. *Rhizocarpon geographicum*. No growth was detected in this species over two and a half growing seasons on Signy Island (1971–72 to 1973–74) at seven different study sites. Since thalli of some species of *Rhizocarpon* have been reported to live for 4 000 years or more (Beschel, 1958, 1961; Denton and Karlen, 1973), it was appreciated that the rate of growth in Antarctic regions must be exceedingly slow and, accordingly, all specimens were marked for future measurement. Re-photography of specimens of *Rhizocarpon geographicum*, *Lecidea* spp. and *Verrucaria ceuthocarpa* in February 1977 has allowed measurement of some thalli following 4 or 5 years' growth (Table III). The mean radial growth rate of *R. geographicum* is shown to be 4 mm century^{-1}, although Lindsay (1973) estimated the radial growth rate of this species on Signy Island to be 8 mm century^{-1}. Some thalli on Signy Island are therefore older than 500–700 years and these growth-rate data have been utilized to date lichenometrically the colonization of the island's moraines (Hooker, 1977).

This study has shown that, although the growth rate of crustose lichens is very slow, as may be expected in the severe environment of the Antarctic, a method of measurement has been employed to resolve not only the mean rate of growth of selected species but also the variation and pattern of growth rate. The influence and importance of some of the environmental variables on growth rate are discussed but it is often difficult to determine which of several interrelated factors has the most direct effect on growth. However, water availability is probably the most important but is closely associated with substratum aspect and availability of mineral and organic nutrients.

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