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SEASONAL GROWTH AND GROWTH RATE–COLONY SIZE RELATIONSHIPS IN SIX SPECIES OF SAXICOLOUS LICHENS

BY R. A. ARMSTRONG

The Botany School, University of Oxford

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SUMMARY

The pattern of seasonal growth and the relation of growth rate to colony size were studied in four foliose and two crustose species of saxicolous lichens. A new method of measuring growth was used whereby the advance of a sample of lobes along millimetres marked on the substrate was measured under a magnification of $\times 10$. Three peaks of growth were found (in March, June and November) for the foliose species and a single peak (in May–August) for the crustose species. The peaks of growth corresponded approximately to peaks of rainfall. Growth rate in relation to increasing colony size fell in a smooth exponential curve when expressed on a cm^2/cm^2/unit time basis. This result is consistent with a linear radial rate for most of the thallus sizes for the six species. There is also evidence for an exponential increase in growth rate initially until about 1.5 cm thallus diameter in two of the species when the linear radial rate is achieved.

INTRODUCTION

Over the last 50 years much data has accumulated on growth rates in lichens (see Hale, 1967). Although generalizations can be made from this data, information on the seasonal pattern of growth and the relationships between growth rate and colony size is lacking. This paper reports on the seasonal pattern of growth in samples of six saxicolous lichens and also on the growth rate of a range of colony sizes.

The published values for lichen growth rates are very low (between 1.5 and 5 mm/year for foliose species) so there is a need to develop accurate methods of measuring growth. Two techniques have been used in the past to measure growth rates in lichens, both have considerable disadvantages in a large-scale investigation of seasonal growth. Tracing the outline of thalli on plastic sheets followed by retracing at a later date has been used by many workers (Rydzak, 1956, 1961; Hale, 1959; Brodo, 1964, 1965). This technique which involves inaccuracies of up to 1 mm is unsuitable except for very long-term investigations. Close-up photography has been used by some workers (Frey, 1959; Phillips, 1969; Hale, 1970). This technique, which can be highly accurate and has been used to measure growth over a period of days (Hale, 1970), involves problems of time and expense when applied to a large-scale project measuring many thalli. A technique is now reported which is accurate enough to record seasonal patterns of growth, is quick and easy, and hence advantageous for use in a large-scale project.

Two units have been used in the measurement of growth rate in lichens. An average radial rate measure has been used by Hale (1959), derived from increments in surface area and secondly percent increase of surface area by Rydzak (1961). Woolhouse (1968) argues that the biologically significant aspect of growth is the growth achieved by a thallus in a given time interval in relation to the already existing area of thallus available for the interception of light. This 'mean relative rate of thallus growth' is analogous with the compound interest law of growth of higher plants. The units of this measure are cm^2/cm^2 for growth and cm^2/cm^2/unit time for growth rate.

Material and methods

Six species of saxicolous lichens were used: four foliose species, *Physcia orbicularis* (Neck.) Poetsch., *Parmelia conspersa* (Ehrh. ex Ach.) Ach. *P. glabratula* ssp. *fuliginosa* (Fr. ex Duby) Laund., and *P. saxatilis* (L.) Ach.; and two crustose species, *Rhizocarpon obscuratum* (Arch.) Massal., and *Lecidia tumida* Massal. Nomenclature in this work conforms to James (1965). The material was obtained from a site in South Merionethshire (Nat. Grid. Ref. SN 9661). The descriptive ecology of the saxicolous lichens at the site has been reported by Armstrong, 1973).

A range of thalli of different diameters was selected for each species from vertically inclined surfaces. Only healthy, non-fragmenting, nearly orbicular thalli were used. These thalli were still attached to their rock substrate (a smooth slate) and the rocks placed face up on flat boards in an exposed, unshaded site in the field near to the origin of the samples. The following numbers of colonies were set up on 1 November 1971: *Physcia orbicular*, twenty-seven; *Parmelia conspersa*, forty-four; *P. glabratula* ssp. *fuliginosa*, forty-four; *P. saxatilis*, sixteen; *Rhizocarpon obscuratum*, five; and *Lecidia tumida*, five.

Measurement of growth

For each thallus the advance of a sample of lobes towards fixed points marked on the substratum in unit time was measured. Using a binocular microscope fitted with a micrometer eyepiece and a magnification of $\times 10$, healthy lobes were selected and distances of 1 mm measured from the tips of the lobes and marked on the substrate with a very fine needle. Between eight and ten lobes were sampled for each colony. After a fixed time the advance of the lobe ends along the graduated millimetres was measured. Additional millimetres were marked as growth of the lobe proceeded. Hale (1970) in his photographic study of a single lobe in *Parmelia caperata* preferred to measure growth from the tip of a lobe to a fixed point on the thallus. In this study the very smooth nature of the substrate enabled the millimetres to be marked accurately and be maintained for periods of up to 2 months. Care was taken to provide enough marked millimetres so that during the period of growth a reference point was not obscured. Using this method and recording growth measurements on a monthly basis, measurements accurate to 0.1 mm can be readily obtained. A marked thallus can be set up using this method in about 10 minutes. Growth measurements for November and December were aberrant and this was assumed to be a 'shock' period. These results were discarded and the first recorded growth of the samples is for January 1972. Measurements were made on the first 3 days of every month for the foliose species and at intervals of 1 month for the foliose species and at intervals of 3 months for the crustose species. The experiment was terminated on 1 January 1973. All growth measurements were made on air dry thalli in the laboratory near the site. Care was taken to keep the time spent by the samples indoors to a minimum. In the field the positions of the rocks were rotated on the boards each month. Meteorological data was obtained from the Welsh Plant Breeding Station, Plas Gogerddan, near Aberystwyth.

Expression of growth

The method of Woolhouse (1968) was used. This expresses growth in relation to the already existing area of thallus in units of cm^2/cm^2. This is calculated as follows. At time zero the area of the thallus is measured using a planimeter and this area A_1 is used to calculate a starting radius r_1 assuming a circular thallus. After a time interval a new radius r_2 is derived where r_2 equals r_1 plus the mean value of radial growth measured from the lobes. This radius r_2 is then used to calculate a new area A_2. The growth in cm^2/cm^2 during the time interval t_1 to t_2 is obtained from the expression:

$$\text{mean relative rate of thallus growth} = \frac{\log A_2 - \log A_1}{t_2 - t_1}.$$

In this study $t_2 - t_1$ is 1 month for foliose and 3 months for crustose species. The value of A_2 at the end of one interval becomes A_1 for the next interval. The growth of the sample is obtained by summing values obtained for all thalli in the sample. The growth rate in cm^2/cm^2/year is obtained by summing all values for the 12 months for each thallus.

Results

Data for rainfall in millimetres and short-wave radiation in calories cm^{-2} for 1972 are shown in Fig. 1. Rainfall was high for most of the year with a main peak in June, low

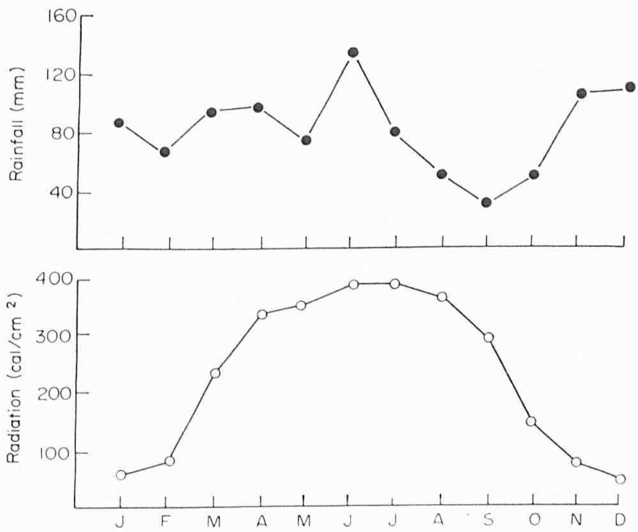

Fig. 1. Distribution of rainfall (●) and short wave radiation (○) at Plas Gogerddan, near Aberystwyth, for 1972.

in the period August–October and then a smaller peak in November–December. The distribution of short-wave radiation was as expected, being high in the months March–September and low in October–February. The growth of the four foliose species for the 12 months of 1972 is shown in Figs. 2 and 3. All four show the same general pattern of growth with a main peak in June, a second peak in November and a third small peak early in the year. The growth of the two crustose species is shown in Table 1. Both show

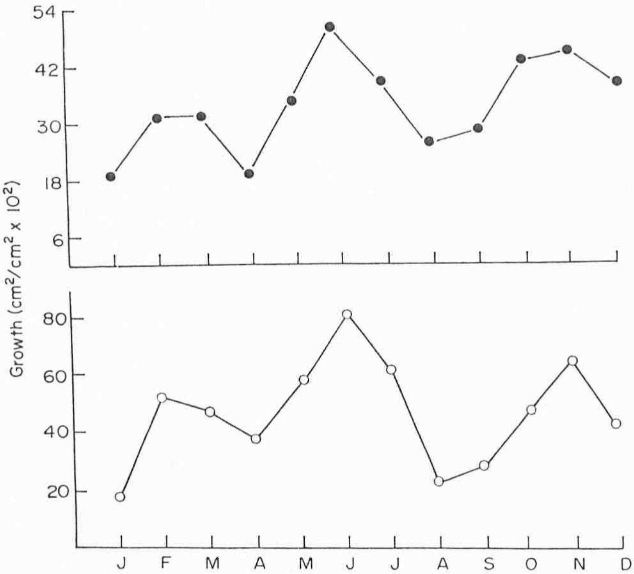

Fig. 2. Seasonal growth pattern of *Physcia orbicularis* (●) and *Parmelia conspersa* (○) for 1972.

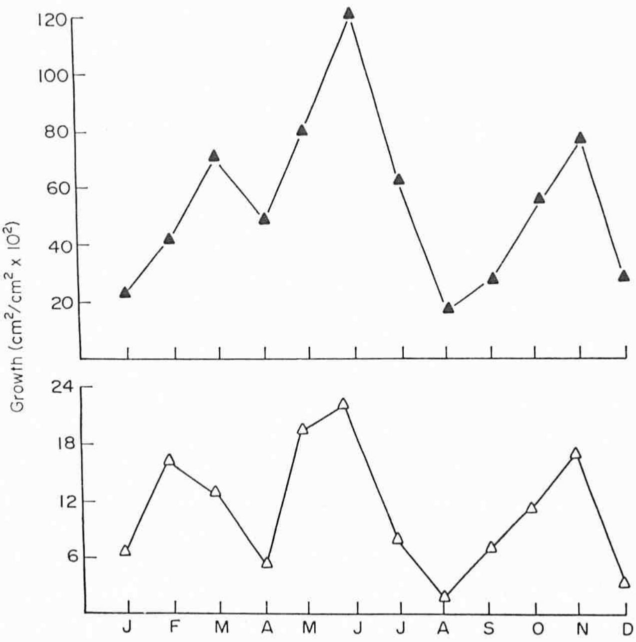

Fig. 3. Seasonal growth pattern of *Parmelia glabratula* ssp. *fulginosa* (▲); and *P. saxatilis* (△) for 1972.

Table 1. *Seasonal growth pattern for two crustose species*

	Growth ($cm^2/cm^2 \times 10^2$)			
	1 Nov. to 1 Feb.	2 Feb. to 1 May	2 May to 1 Aug.	2 Aug. to 1 Nov.
Rhizocarpon obscuratum	0	8.48	10.44	4.64
Lecidea tumida	0.40	3.00	15.36	4.94

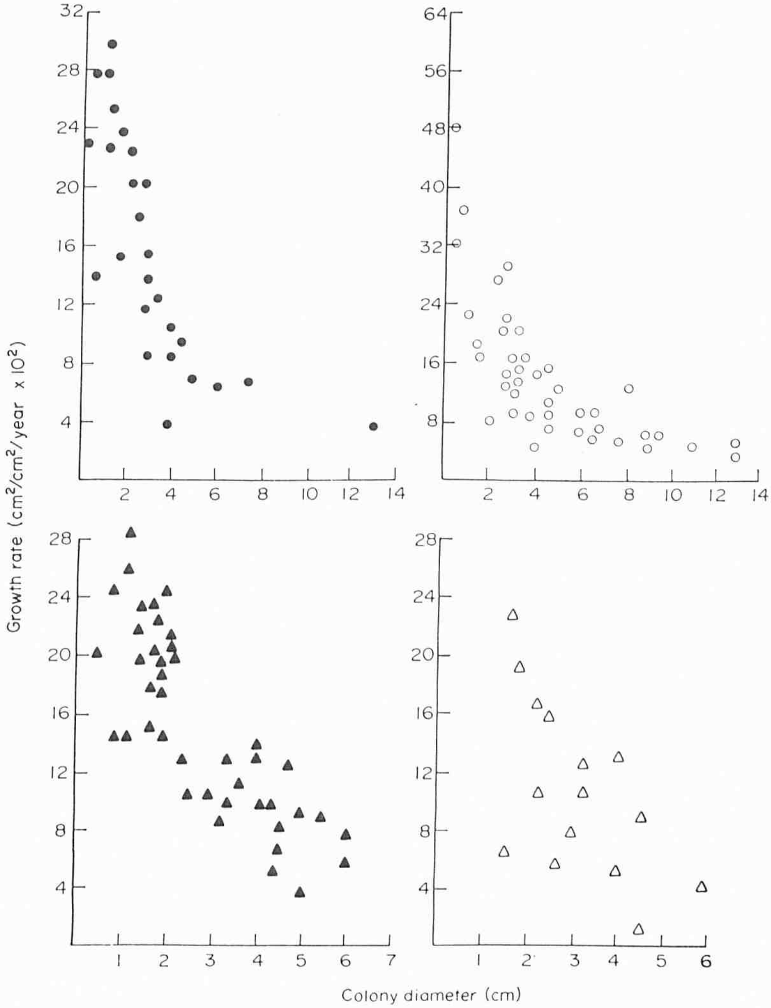

Fig. 4. Growth rate in relation to colony diameter for *Physcia orbicularis* (●); *Parmelia conspersa* (○); *P. glabratula* ssp. *fuliginosa* (▲); and *P. saxatilis* (△).

the same pattern with a peak in the May–August period, and low growth in November–February. The growth rate in cm^2/cm^2/year in relation to initial colony diameter for the four foliose species is shown in Fig. 4. The theoretical expectation of growth of a thallus growing at a linear rate (5 mm/year) throughout its life is shown in Fig. 5. This average linear radial rate gives a smooth exponential curve when expressed in units of cm^2/cm^2/

unit time. The results for the four foliose species indicate that for most of the life of the thallus the growth rate is linear. There is some evidence in *Physcia orbicularis* and *Parmelia glabratula* ssp. *fuliginosa* that growth was slower than the linear rate at the early stages of thallus growth up to a diameter of 1.5 cm in both species. This was not observed in *P. conspersa* and *P. saxatilis*. The growth rate in relation to colony

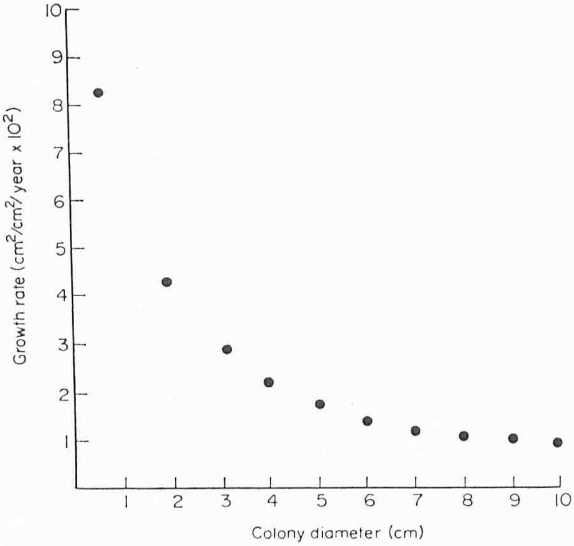

Fig. 5. Theoretical expectation of growth of a thallus growing at a linear rate (5 mm/year) throughout its life.

Table 2. *Growth rate in relation to colony diameter for two crustose species*

Colony diameter (cm)	Growth rate ($cm^2/cm^2/year \times 10^2$) *Rhizocarpon obscuratum*	*Lecidea tumida*
0.6	13.06	–
0.8	–	12.19
1.0	2.63	–
1.5	3.00	–
2.0	1.85	6.00
2.2	–	3.66
2.5	–	1.24
3.0	3.02	–
3.5	–	0.61

diameter for the two crustose species is shown in Table 2. Highest growth rate was found in the smallest thalli and growth rate decreased with increasing colony size like the foliose species.

DISCUSSION

Seasonal variation in growth of lichens was predicted by Smith (1962). He showed a cyclic variation in respiration rate during the year with peaks in spring and autumn, coinciding with periods of optimal photosynthetic activity, in the corticolous material used. The first evidence of seasonality in growth obtained in the field was the study of Rydzak (1961) in Poland where lichen growth practically ceased during the winter and 'best' growth was found in cool wet summers. Phillips (1963) measured thalli of *Parmelia conspersa* and showed that the summer growth rate was approximately six times the winter growth rate. The most detailed work on seasonal growth has been reported by Hale (1967, 1970). In this work two saxicolous lichens were studied for a period of months and considerable month-to-month variation in growth was reported correlated with precipitation rather than temperature (Hale, 1967). In addition he photographed a single lobe of *P. caperata* at intervals of a few days for 1 year and showed that growth occurred throughout the year but was most rapid in May–June and consistently low from December–March (Hale, 1970). Some but not all of the quadrats he studied showed a second high peak of growth in the period October–November. The data reported in this paper on 1 year's observations agree with that of Hale (1970) in showing a major peak in June and a secondary peak in November. These two peaks correspond to the two peaks of precipitation occurring during the year. In detail, however, the seasonal growth pattern is not exactly mirrored by that of precipitation, e.g. there is a fall in total growth of the samples in April and a rise in September not directly related to changes in precipitation. Other factors such as light intensity, temperature and nutrient supply may also affect the seasonal growth pattern. A number of studies have emphasized the importance of water availability and light intensity for optimal photosynthesis and growth (e.g. Harris, 1971; Karenlampi, 1971). Some evidence is also available from a preliminary study of seasonal variations in nutritient content of precipitation at the site (R. A. Armstrong, unpublished). No earlier reports exist on the seasonal pattern of growth in crustose species. The results reported here suggest that the growth pattern is similar to that of the foliose species.

Little data has been reported on the relationship between colony size and growth rate. Rydzak (1961) stated that smaller thalli appeared to have a faster rate of growth than larger thalli basing his results on total surface area increments. Hale (1967) studied mature and juvenile thalli of *P. conspersa* and, expressing his results as radial rates, showed significantly slower growth in the juvenile thalli. In addition a sigmoid pattern of growth in the lichen was demonstrated, growth being slow until a diameter of 1.0–1.5 cm was reached, then growth was linear until about 12 cm when a noticeable slowing occurred. A second pattern has been shown when growth measurements were obtained from dated substrates, e.g. gravestones (Platt and Amsler, 1955; Beschel, 1958). In this case radial growth after a brief lag period was most rapid in juvenile thalli reaching a a peak in individuals between 4 and 8 years old after which the rate became linear through to maturity. In this study a linear radial rate or an exponential curve in $cm^2/cm^2/$ unit time is shown for most of the thallus sizes greater than 1.5 cm. There is evidence of a slower growth rate in juvenile thalli until a diameter of 1.5 cm is reached when the linear rate is achieved. These results agree with those of Hale (1967). However, a slowing of the linear radial rate in mature thalli was not observed. This slowing of growth rate in Hale's work corresponds to a fragmenting of the thallus (Hale, 1967) and would not be noticed in this study since only healthy non-fragmenting thalli were used. The critical period of growth occurs in juvenile thalli during establishment and the growth phase before the linear radial rate is achieved. Beschel (1961) states that this early growth is logarithmic after a brief lag phase during establishment. Early logarithmic growth is also indicated by the dry weight data of Platt and Amsler (1955) obtained from foliose epiphytic lichens. As a consequence of this early growth phase accurate data on thallus age cannot be obtained by simple extrapolation from the linear rate. This is because no information is available on the duration of the lag phase or the logarithmic phase and hence lichen thalli will be much older than the estimates quoted by many workers. Further work on the growth rates of young establishing thalli and on the log phase of growth is needed. In units of cm^2/cm^2 growth rises to a peak at about 1.5 cm and then falls away in an exponential curve as a linear radial rate is established. The onset of this linear rate phase is interpreted by Beschel (1961) in terms of a balance between central and marginal growth. In young thalli (1.5 cm) almost all productivity goes into marginal growth. As the thallus increases in size lateral transport of material from edge to centre is inhibited, the thallus becomes thicker and produces reproductive structures (soredia, isidia or apothecia). Consequently, less material is put into lateral growth and marginal increase is not so rapid. Ultimately a balance is met between central and marginal growth and radial growth becomes linear. Finally fragmentation of the centre occurs and this corresponds to a slowing of the linear radial rate.

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REFERENCES

Armstrong, R. A. (1973). The descriptive ecology of saxicolous lichens in South Merionethshire. *J. Ecol.* (in press).

Beschel, R. (1958). Flechtenvereine der Städte, Stadtflechten und ihr Wachstum. *Ber. naturw.-med. Ver. Innsbruck*, **52**, 1.

Beschel, R. (1961). Dating rock surfaces by lichen growth and its application to glaciology and physiography (lichenometry). In: *Geology of the Arctic*, Vol. 2, p. 1044. University of Toronto Press, Toronto.

Brodo, I. M. (1964). Field studies of the effects of ionising radiation on lichens. *Bryologist*, **67**, 76.

Brodo, I. M. (1965). Studies on growth rates of corticolous lichens on Long Island, New York. *Bryologist*, **68**, 451.

Frey, E. (1959). Die Flechtenflora und -vegetation des National-parks in Unterengardin. II Teil: Die Entwicklung der Flechtenvegetation auf photo-grammetrisch kontrollierten Dauerflachen. *Ergebn. wiss. Unters. schweiz. NatnParks*, N.F. **6**, 241.

Hale, M. E. Jnr (1959). Studies on lichen growth rate and succession. *Bull. Torrey bot. Club*, **66**, 126.

Hale, M. E. Jnr (1967). *The Biology of Lichens*. Arnold, London.

Hale, M. E. Jnr (1970). Single-lobe growth rate patterns in the lichen *Parmelia caperata*, *Bryologist*, **73**, 72.

Harris, G. P. (1971). The ecology of corticolous lichens. II. The relationship between physiology and the environment. *J. Ecol.*, **59**, 441.

James, P. W. (1965). A new check-list of British lichens. *Lichenologist*, **3**, 95.

Kärenlampi, L. (1971). Studies on the relative growth rate of some fruticose lichens. *Rep. Kevo Subarctic Res.*, **7**, 33.

Phillips, H. C. (1963). Growth rate of *Parmelia isidiosa* (Mull. Arg.) Hale. *J. Tenn. Acad. Sci.*, **38**, 95.

Phillips, H. C. (1969). Annual growth rates of three species of foliose lichens determined photographically. *Bull. Torrey. bot. Club*, **96**, 202.

Platt, R. B. & Amsler, F. P. (1955). A basic method for the immediate study of lichen growth rates and succession. *J. Tenn. Acad. Sci.*, **30**, 177.

Rydzak, J. (1956). A method of studying growth in lichens. *Annls Univ. Mariae Curie-Sklodowska*, **10**, 87.

Rydzak, J. (1961). Investigations on the growth rate of lichens. *Annls Univ. Mariae Curie-Sklodowska*, **16**, 1.

Smith, D. C. (1962). The biology of lichen thalli. *Biol. Rev.*, **37**, 537.

Woolhouse, H. W. (1968). The measurement of growth rates in lichens. *Lichenologist*, **4**, 32.