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Lobe Growth Variation and the Maintenance of Symmetry in Foliose Lichen Thalli

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Abstract

The aim of this study was to determine how thallus symmetry could be maintained in foliose lichens when variation in the growth of individual lobes may be high. Hence, the radial growth of a sample of lobes was studied monthly, over 22 months in 7 thalli of *Parmelia conspersa* (Ehrh. ex Ach.) Ach. and 5 thalli of *P. glabratula ssp. fuliginosa* (Fr. ex Duby) Laund. The degree of variation in the total radial growth of different lobes within a thallus over 22 months varied between thalli. Individual lobes showed a fluctuating pattern of radial growth from month to month with alternating periods of fast and slow growth. Monthly variations in radial growth of different lobes were synchronised in some but not in all thalli. Few significant correlations were found between the radial growth of individual lobes and total monthly rainfall or shortwave radiation. The levels of ribitol, arabitol and mannitol were measured in individual lobes. All three polyols varied significantly between lobes within a thallus suggesting that variations in algal photosynthesis and in the partitioning of fungal polyols may contribute to lobe growth variation. The effect on thallus symmetry of lobes which grew radially either consistently faster or slower than average was studied. Slow growing lobes were overgrown, and gaps in the perimeter were eliminated by the growth of neighbouring lobes, in approximately 7 to 9 months. However, a rapidly growing lobe, with its neighbours removed on either side, continued to grow radially at the same rate as rapidly growing control lobes. The results suggest that lobe growth variation results from a combination of factors which may include the origin of the lobes, lobe morphology and the patterns of algal cell division and hyphal elongation in different lobes. No convincing evidence was found to suggest that exchange of carbohydrate occurred between lobes which would tend to equalise their radial growth. Hence, the fluctuating pattern of lobe growth observed may be sufficient to maintain a degree of symmetry in most thalli. In addition, slow growing lobes would tend to be overgrown by faster growing neighbours thus preventing the formation of indentations in the thallus perimeter.

Keywords: *Parmelia conspersa*, *P. glabratula ssp. fuliginosa*, lobe growth variation, thallus symmetry

1. Introduction

A number of studies have reported variations in the radial growth of different lobes in foliose lichen thalli. Phillips (1969) investigated patterns of lobe growth in three foliose species and found, in individual thalli, that some lobes grew radially, two and a half times the average for the year, while others showed no measurable growth. In addition, Lawrey and Hale (1977) and Benedict and Nash (1990) found that radial growth varied markedly from lobe to lobe. Lobe growth variation may result from the relative independence of radial growth of individual lobes in the thallus perimeter (Jones and Platt, 1969; Armstrong, 1982; 1984). Few studies have considered the causes of lobe growth variation and its effect on thallus symmetry in foliose lichens. However, several explanations for thallus symmetry have been proposed. First, slow growing lobes may be overgrown by faster growing neighbours; a mechanism observed by Hooker (1980) in *Xanthoria elegans* (Link)Th.Fr. In this species, one in four of the peripheral lobes was unable to grow fast enough to keep up with the advancing periphery. Hence, an indentation in the thallus perimeter, resulting from slow radial growth, would be removed. Second, different lobes may show similar patterns of radial growth over time either because they were morphologically similar i.e. of similar width (Hill, in press) or growth was correlated with seasonal changes in climate (Armstrong, 1973; 1988). Third, individual lobes may grow differently in successive months. Hence, some lobes may grow faster in one month and slower in the next and vice versa. These differences may be due to the lobes growing relatively independently of each other and could be due to variations in algal cell division or hyphal elongation in different lobes (Slocum et al., 1980). Alternatively, they could represent a compensatory mechanism by which the radial growth of rapidly growing lobes could be reduced and the growth of slow lobes compensated. A possible mechanism, which could equalise lobe growth, is the exchange of carbohydrate. A prediction of the Aplin and Hill growth model (Aplin and Hill, 1979; Hill, 1981), which explains several features of the radial growth of circular lichen thalli, is that if slow growth resulted in an indentation in the perimeter, local carbohydrate concentration would rise to enable more rapid growth thus eliminating the indentation. Exchange of carbohydrate between lobes could occur through fungal hyphae or by the release of carbohydrate after wetting and subsequent reabsorption (Farrar and Smith, 1976).

The major objectives of this study were: (1) to study the pattern of lobe growth variation in several thalli over short intervals of time to determine whether lobes grew independently of each other or whether a mechanism was present to equalise lobe growth; (2) to measure the levels of carbohydrates in individual lobes to determine whether variations in the production of ribitol and/or arabitol and mannitol might contribute to lobe growth variation and; (3) to study the effects on thallus symmetry of lobes which grow consistently faster or slower than average.

2. Materials and Methods

Site and lichens

The study was carried out at a site in South Gwynedd, Wales, UK (Nat. Grid Ref. SN 6196) described previously (Armstrong, 1974). Unless otherwise stated, all studies were made using approximately symmetrical thalli of *Parmelia conspersa* (Ehrh. ex Ach.) Ach. or of *P. glabratula ssp. fuliginosa* (Fr. ex Duby) Laund. without fragmenting centres. Thalli were removed from various south facing rock surfaces on pieces of smooth slate which were placed on horizontal boards in an unshaded site in the field. The majority of thalli observed on these rock surfaces showed a considerable degree of symmetry and many were approximately circular in shape. Thalli were placed on the boards for at least a year before they were used in a study.

Climatic records

Data on total monthly rainfall (mm) and mean daily shortwave radiation (cal/cm^2) in the period 1, Oct. 1983 to 1, Aug. 1985 were obtained from the Welsh Plant Breeding Station, Plas Gogerddan, near Aberystwyth, 8 miles to the south and at the same altitude as the sample site.

Lobe growth variation

Variation in the growth of individual lobes was studied monthly in 7 thalli of *P. conspersa* and 5 thalli of *P. glabratula ssp. fuliginosa.* Between 5 and 8 major lobes were selected from each thallus at random for detailed study.

The radial growth of each of the 75 lobes studied was measured at the beginning of each month for 22 months from 1, Oct. 1983 until 1, Aug. 1985 using previously described methods (Armstrong, 1973). Four statistical analyses were made on the data. First, the growth increments over 22 months were totalled for each lobe. The standard deviation (SD) and the coefficient of variation (CV) were calculated for each thallus to determine the level of lobe growth variation over the period of the study. Second, the data for each thallus were analysed by a two-way (lobes and months) analysis of variance (Snedecor and Cochran, 1980). The total variance was partitioned into components i.e. the proportion of the total variance attributable to lobes, months and lobes $\times$months was calculated. The lobes $\times$ months variance measures the degree to which differences in the growth of a series of lobes were maintained in successive months. If this component of variance was high it might indicate that lobes grew relatively independently of each other. Alternatively, it could also indicate the presence of a compensatory mechanism which would balance the growth of different lobes. Third, to test whether individual lobes showed similar monthly patterns of growth, the degree of correlation between the growth of all measured lobes in a thallus was determined by calculating a Pearson's correlation coefficient matrix for each thallus. Fourth, the degree of correlation between monthly measurements of radial growth and total rainfall and mean daily shortwave radiation was tested for each lobe (Armstrong, 1973; 1988).

Levels of polyols in individual lobes

In lichens with *Trebouxia* as the phycobiont, carbohydrate is released from the alga as ribitol and is then converted into arabitol and mannitol in the fungus (Farrar, 1976). Lobe growth variation could be attributable to variations in the production of ribitol in individual lobes and/or in the way that the carbohydrate transferred to the fungus is partitioned between growth and the storage polyols arabitol and mannitol. Hence, the levels of ribitol, arabitol and mannitol were measured in individual lobes of *P. conspersa* thalli. Two populations of *P. conspersa* thalli were investigated one from a steep north and the other from a south facing rock surface at the study site. Four lobes of similar width and length were cut from each of 4 thalli chosen at random from each population. Samples were collected on 4 occasions from each site: 30, May, 7, July; and 1, Dec. 1990 and 4, Apr. 1991. Individual lobes were stored in 80% ethanol in a refrigerator before analysis.

Carbohydrates were determined by gas chromatography using the method described in detail by Armstrong and Smith (1987). In essence, carbohydrates were extracted from each lobe by refluxing in 80% (v/v) ethanol. Subsequently, extracts were silylated and then characterised by capillary gas chromatography. Levels of individual carbohydrates were determined by reference to an internal standard added at the initial extraction stage.

In this study, the degree of variation in carbohydrates between individual lobes in a thallus was of particular interest. Hence, the data for each carbohydrate at each sampling time were analysed by analysis of variance of a nested classification with partitioning of the total variance into components i.e. variance between lobes within individual thalli, between individual thalli within a sample site and between sites (Snedecor and Cochran, 1980).

The effect of slow growing lobes on thallus symmetry

If individual or groups of lobes grow radially more slowly than their neighbours then indentations in the thallus margin would develop. The purpose of this experiment was firstly, to determine whether slow growing lobes would be overgrown by faster growing neighbours as observed by Hooker (1980) and secondly, how quickly gaps in the thallus margin would be eliminated. On 1, Jan. 1984 three lobes were chosen from each of eight thalli of *P. conspersa*. At random, one lobe was chosen as the control. One was partially painted with a thin layer of acrylic paint (Liquitex Brand, Binney and Smith Inc., Easton, PA 18042, USA) mixed to a similar shade as the colour of the thallus to reduce reflectivity changes. The lobe was painted from the point where it merged into the centre of the thallus to within 1 mm of the tip. Previous experiments suggested that this treatment reduces radial growth of a lobe to about 30 to 40% of the unpainted control lobes in *P. conspersa* (Armstrong, 1991). Finally, the remaining lobe was removed from the thallus by cutting its base with a scalpel creating a gap 3 to 5 mm in width. The radial growth of both lobes adjacent to the painted and cut lobes was measured (Armstrong, 1973) at two monthly intervals until Jan. 1985. In addition, for the latter treatment, the area of the gap was measured at each sampling time by tracing the outlines of the adjacent lobes on to "clingfilm".

The effect of rapidly growing lobes on thallus symmetry

Thallus asymmetry could also result from lobes growing consistently faster than their neighbours. The purpose of this experiment was to test the hypothesis that the radial growth of a rapidly growing lobe would decline as it grew beyond the margin of the perimeter because either: (1) the lobe would be growing in a more exposed microenvironment (Armstrong, 1984) or (2) the lobe would tend to increase in width rather than continue to grow exclusively in the radial direction (Armstrong, 1991). On 1, Apr. 1990, 3 particularly fast growing lobes were identified from each of eight *P. conspersa* thalli. At random, one lobe was chosen as the control and, for the remaining two lobes, at least two neighbouring lobes were removed from either side. Hence, the experimental lobes extended beyond their cut neighbours by between 4 to 6 mm. The radial growth and width of each lobe were measured, the latter measured by vernier calipers 0.5 mm behind the lobe tip.

3. Results

The total radial growth of each lobe from each thallus measured over 22 months is shown in Table 1. The degree of lobe growth variation present over this period varied between thalli (CV in *P. conspersa* 9–27%; *P. glabratula ssp. fuliginosa* 10–36%). In some of the thalli (e.g. PC/7, PG/2, PG/5) individual lobes grew considerably slower or faster than others. There is no relationship between the degree of lobe growth variation as measured by the SD

Table 1. Total radial growth (mm) of individual lobes of *Parmelia conspersa* (PC) and *Parmelia glabratula ssp. fuliginosa* (PG) over 22 months. ($\bar{X}$ = mean; SD = standard deviation, CV = coefficient of variation %)

		Lobe number										
Thallus	Size (cm)	1	2	3	4	5	6	7	8	$\bar{X}$	SD	CV
PC/1	8.2	6.2	7.2	9.4	7.4	7.0	8.3	–	–	7.6	1.1	14
PC/2	6.0	6.0	6.8	3.9	6.1	6.0	6.0	–	–	5.8	0.9	17
PC/3	9.5	3.8	4.3	7.3	4.9	4.9	–	–	–	5.0	1.3	27
PC/4	13.0	3.5	3.9	3.9	4.2	2.9	2.3	3.3	2.3	3.3	0.7	22
PC/5	2.4	5.5	5.0	4.8	6.0	4.9	–	–	–	5.2	0.5	9
PC/6	11.0	3.4	5.7	5.0	4.0	4.5	4.8	4.3	–	4.5	0.7	16
PC/7	4.5	2.0	4.0	2.1	3.5	3.2	2.7	–	–	2.9	0.8	27
PG/1	4.5	6.1	3.5	5.1	2.4	4.8	4.7	–	–	4.4	1.3	29
PG/2	4.0	1.2	5.1	5.2	4.8	4.5	4.1	–	–	4.1	1.5	36
PG/3	2.0	3.2	3.8	4.0	3.2	2.9	2.8	–	–	3.3	0.5	14
PG/4	4.3	3.2	3.0	3.3	3.9	2.9	3.7	3.1	3.2	3.3	0.3	10
PG/5	4.0	4.1	3.0	4.3	1.8	3.2	3.9	–	–	3.4	0.9	27

Table 2. Analysis of variance of the radial growth of different lobes in thalli of (PC) *Parmelia conspersa* and (PG) *Parmelia glabratula ssp. fuliginosa* (F = variance ratio, components of variance × 10^{-2}: σ^2L=Lobes; σ^2M=Months; σ^2LM=Lobes ×Months; ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$).

Thallus	Size (cm)	F, Lobes	F, Month	σ^2L	σ^2M	σ^2LM
PC/1	8.2	0.39	2.29**	0	0.015	7.1
PC/2	6.0	0.64	0.97	0	0	6.8
PC/3	9.5	1.8	1.4	0.02	0.4	5.3
PC/4	13.0	0.46	3.53***	0	1.6	5
PC/5	2.4	0.2	2.18*	0	1.5	6.5
PC/6	11.0	0.46	2.13*	0	1.1	6.6
PC/7	4.5	1.23	6.05***	0.04	2.3	2.8
PG/1	4.5	1.72	1.34	0.078	0.25	4.4
PG/2	4.0	3.25*	3.26***	0.36	1.2	3.2
PG/3	2.0	0.39	1.53	0	0.4	5
PG/4	4.3	0.17	2.79***	0	0.84	3.7
PG/5	4.0	1.43	1.99*	0.7	0.52	3.2

or CV and thallus diameter. The analyses of variance (Table 2) indicated (1) that a statistically significant difference between the growth of individual lobes over 22 months was present in only one thallus (PG/2); (2) that significant growth period differences were evident in 8/12 thalli; and (3) that in all thalli the largest component of variance was that attributed to lobes × months i.e. differences between lobes were not consistent from month to month. Hence, most lobes do not grow consistently faster or slower than their neighbours but over a period of time show a more fluctuating pattern with alternating periods of fast and slow growth. An example of this pattern of growth is shown by thallus PC/1 (Fig. 1). The fluctuating pattern in the different lobes is clearly evident with some of the peaks being in phase.

Examination of the Pearson's correlation matrices (Table 3) indicates that out of a total of 202 pairs of lobes tested from all thalli, 38 (19%) of the pairs were positively correlated. A single negative correlation was found between the lobes tested. Positive correlations were more common in some thalli (e.g. PC/1, PC/4, PC/7) than in others (e.g. PC/2, PC/3). The radial growth of lobes located closest together in the thallus perimeter were more likely to be positively correlated. Lobe growth correlated poorly with the climatic factors

Table 3. Significant correlations (Pearson's 'r') between the radial growth of the lobes from each thallus of (PC) *Parmelia conspersa* and (PG) *Parmelia glabratula ssp. fuliginosa* and between growth and total monthly rainfall (R) and mean shortwave radiation (SW)

Thallus	Size (cm)	Number of lobes	Number of pairs	Significant correlations +	Significant correlations −	R	SW
PC/1	8.2	6	15	8	0	2(+)	0
PC/2	6.0	6	15	1	0	0	0
PC/3	9.5	5	10	1	0	1(+)	0
PC/4	13.0	8	28	6	1	0	0
PC/5	2.4	5	10	1	0	0	1(−)
PC/6	11.0	7	21	1	0	1(+)	2(−)
PC/7	4.5	6	15	10	0	0	0
PG/1	4.5	6	15	1	0	1(+)	0
PG/2	4.0	6	15	3	0	1(+)	0
PG/3	2.0	6	15	1	0	0	0
PG/4	4.3	8	28	4	0	2(+)	0
PG/5	4.0	6	15	1	0	2(+)	0

tested; 10/75 lobes were positively correlated with total rainfall while 3/75 lobes were negatively correlated with shortwave radiation.

Mean levels of polyols (μg/lobe) in individual lobes from all thalli at the 4 sample times are shown in Table 4. The levels of arabitol and mannitol were similar and approximately three times the level of ribitol. Analysis of polyol levels in individual lobes suggested that there were considerable variations between lobes within a thallus (Table 5) with variations in the fungal polyols being especially large. Variations between individual thalli were small compared with lobe to lobe variation. In addition, significant variations between samples collected from north and south facing rock surfaces were found at some sample times, e.g. arabitol on 7, July 1990 and mannitol on 30, May 1990.

Radial growth of an individual lobe was reduced compared to control lobes by partially painting its surface. These slower growing lobes were overgrown by their neighbours within approximately 7 to 9 months after the painting treatment. In addition, gaps in the perimeter, created by removing individual lobes, were eliminated in a similar time period (Table 6). The radial growth of the lobes adjacent to either the partially painted or removed lobes was similar

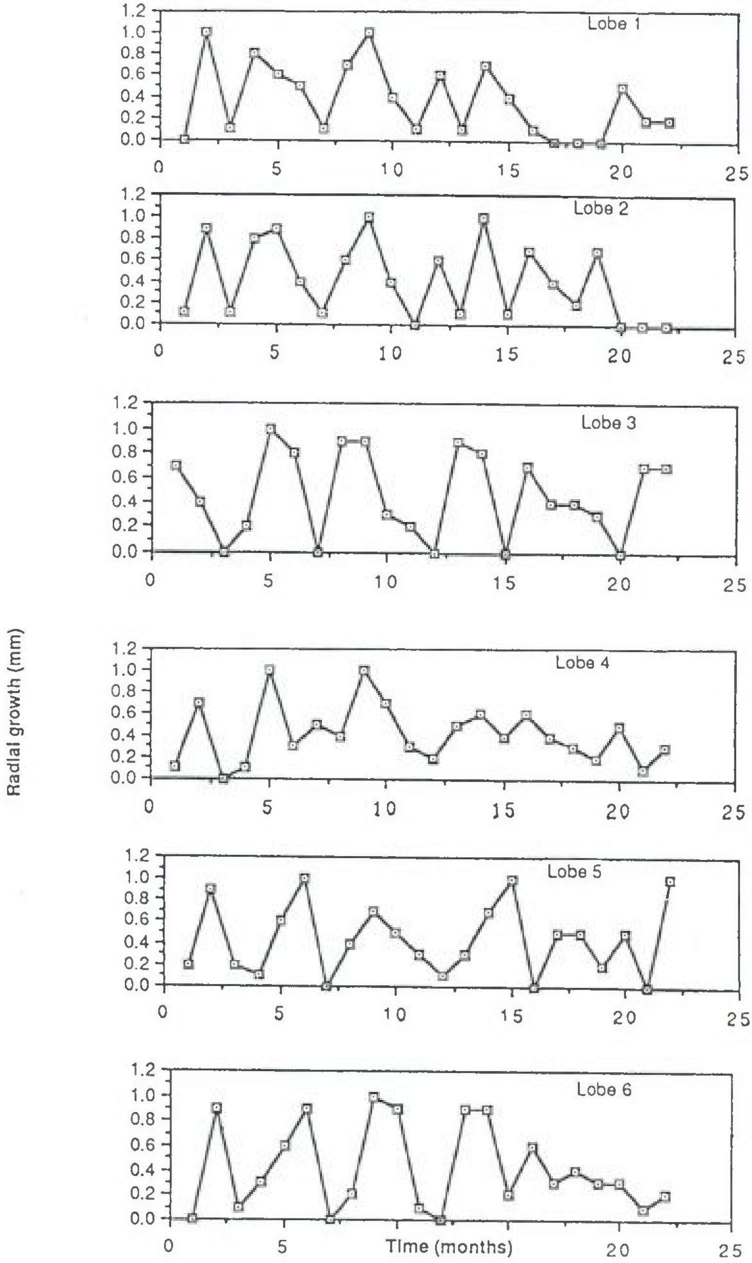

Figure 1. Radial growth (mm) in each of 22 successive months of 6 lobes of *Parmelia conspersa* from thallus PC/1

Table 4. Mean levels of ribitol, arabitol and mannitol (μg/lobe) in individual lobes from all thalli at four sample times

	Polyol	
Ribitol	Arabitol	Mannitol
7.26	19.78	19.66

Table 5. Components of variance of polyol levels in individual lobes of thalli of *Parmelia conspersa* (Variance attributable to: σ^2L between lobes within thalli; σ^2T between thalli within sample sites and σ^2N/S between sample sites)

Sample	Polyol	σ^2L	σ^2T	σ^2N/S
May 1990	ribitol	11.74	1.96	0.89
	arabitol	85.53	3.66	7.98
	mannitol	79.88	1.09	20.17
July 1990	ribitol	7.02	1.11	0.91
	arabitol	23.14	2.6	18.85
	mannitol	47.45	2.91	8.67
Dec. 1990	ribitol	7.51	3.47	0.88
	arabitol	80.14	0.52	8.51
	mannitol	361.75	17.63	7.1
April 1991	ribitol	11.04	0.54	3.12
	arabitol	94.50	29.39	4.67
	mannitol	66.09	20.18	34.62

to that of control lobes. However, in each case there was a significant increase in the width of adjacent lobes during the experiment. The radial growth of rapidly growing lobes over 12 months with neighbours removed on either side was similar to rapidly growing control lobes and did not decrease over the experimental period. As in the previous experiment, the width of the isolated lobes increased over this period compared with control lobes (Table 7).

4. Discussion

The results suggest that lobe growth variation in foliose thalli may be due to several causes. First, the degree of variation present varied between thalli.

Table 6. The effect on radial growth (mm in 1 yr; standard errors in parentheses) of *Parmelia conspersa* of slowing the rate of radial growth of adjacent lobes and creating gaps by removing lobes from the thallus

	Control	Painted lobe	Lobes adjacent to painted lobes	Lobes adjacent to removed lobes
Radial growth (mm)	2.28 (0.27)	0.075 (0.06)	1.94 (0.17)	2.2 (0.22)
Time to remove gap (months)	—	—	9.4 (0.45)	8.8 (0.36)

Analysis of variance (two way) growth data (painted lobe data not included) F = 1.23 (P > 0.05).

Table 7. The effect on mean radial growth (mm in 1 yr; standard errors in parentheses) and change in lobe width (mm) of rapidly growing lobes of *Parmelia conspersa* when adjacent lobes were removed

	Control	Adjacent lobes removed
Radial growth (mm in 1 yr)	1.8 (0.27)	1.59 (0.23)
Change in lobe width (mm)	0.19 (0.03)	2.53 (0.04)

Comparison between means: Growth data 't' = 1.08 (P > 0.05); width data 't' = 3.75 (P < 0.01).

This may be due to the genetic origin of lobes in a thallus. Lobes may result from the division of a single "parent" lobe or fragment (Armstrong, 1981) or lobes from different individuals could combine together to form a single thallus (Armstrong, 1984). This could occur, for example, in cracks in a substratum where propagules from several individuals may collect. Hence, lobes with a single 'genetic' origin may show less variation than lobes of different origin. Second, the morphology of the lobe may be an important factor. Radial growth rate may be related to lobe width, i.e. wide lobes grow faster than narrow lobes (Benedict and Nash, 1990; Hill, in press) and thalli frequently comprise lobes of different widths. Hence, lobe growth variation may reflect the distribution of lobe widths present in the thallus. Third, lobe growth variation could be due to differences in the behaviour of algal cells or fungal hyphae. Algal cells divide more frequently at the tips of lobes than in the centre of the thallus (Greenhalgh and Alglesea, 1979); a process that may be sensitive to the local microclimate of the lobe. Zoosporogenesis has been observed in hydrated sections of *Parmelia conspersa* (L.) Ach. which was not synchronised within the thallus (Slocum et al., 1980). In addition, the fungal hyphae at the margin of a lobe have longer cells and thinner walls than in the medulla (Boissière, 1972) and hence, it is possible that elongation of these hyphae may occur at different rates in different lobes. Variations in the levels of polyols between individual lobes of similar length and width were large. Differences in the levels of ribitol may reflect differing rates of algal photosynthesis in the lobes which, in turn, may be related to the pattern of division of the algal cells. Variations in the fungal polyols between lobes were especially large suggesting differences in the way polyols were partitioned and utilised. Arabitol and mannitol may facilitate growth by acting as an energy source or by protecting macromolecules during stress (Farrar and Smith, 1976). Hence, fluctuations in the levels of these polyols could contribute to the fluctuating pattern of growth observed in individual lobes and to lobe growth variation. Alternatively, polyol variation could be the result rather than a cause of lobe growth variation; the levels increasing during periods of low radial growth and decreasing during periods of more rapid growth.

In some thalli the majority of lobes appear to grow relatively independently of each other with little evidence of a coordinating mechanism. However, it is possible that compensatory adjustments may occur within shorter periods than a month or over a longer time interval than 22 months and would not be detected by the present analysis. In other thalli positive correlations between the growth of lobes were more common particularly between lobes located close together. This could be due to the lobes sharing a common origin i.e. resulting from the division of a single "parent" lobe. It is also possible that the positive correlations arise because the radial growth of different lobes was correlated with changes in local climate. Few such correlations were found in this study but the climatic data were not extensive enough to test the importance of this factor fully. Alternatively, the correlations could result from a compensatory mechanism tending to equalise the growth of neighbouring lobes. An additional factor which may be important in determining the fluctuating pattern of growth is the pattern of lobe branching (Hill, in press). If radial growth is related to lobe width as demonstrated by Hill (in press), then lobes may show alternating periods of faster and slower growth as the lobes grow and then divide. In addition, if the pattern of lobe division is not synchronised in different parts of the thallus then the pattern of lobe growth variation could vary from month to month. Further experiments will be necessary to test this hypothesis.

The data suggest that although an obvious integrating mechanism appears to be absent, a number of processes contribute to thallus symmetry which may vary in importance in individual thalli. First, in many thalli the lobes show a non synchronised pattern of fluctuating radial growth from month to month. This pattern of radial growth would tend to result in symmetrical growth over a long period in foliose thalli because monthly variations in lobe growth cancel out. Second, in some thalli, positive correlations between the growth of different lobes, possibly determined either by their origin or by mutual correlations with climatic factors, may contribute to thallus symmetry. Third, despite these factors, over 22 months, some individual lobes will grow consistently slower than the average for the thallus. The data show that such a lobe would be overgrown by faster growing neighbours as suggested by Hooker (1980). In addition, if indentations did develop in the perimeter then they would be removed by the increase in lobe width of neighbouring lobes. However, the data fail to demonstrate that a rapidly growing lobe would slow down when it grows beyond the perimeter at least over the period of the experiment. It is possible that as the lobe divides its growth would be slowed sufficiently to allow neighbours to catch up, thus preventing the development of outgrowths or "buds" on the thallus perimeter. Hence, a relatively undifferentiated lichen thallus, which shows more or less independent growth at any point on the colony, can achieve a degree of symmetry without an obvious integrating homeostatic mechanism.

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