Symbiosis, 26 (1999) 265–277
Balaban, Philadelphia/Rehovot

Factors Associated with Lobe Division in the Lichen *Parmelia conspersa* (Ehrh. ex. Ach.)Ach.

R.A. ARMSTRONG[1*] and S.N. SMITH[2]
[1]*Vision Sciences, and* [2]*Pharmaceutical and Biological Sciences, Aston University, Birmingham B4 7ET, UK, Tel. +44-121-3593611, Fax. +44-121-3334220, E-mail. R.A.Armstrong@aston.ac.uk*

Received March 27, 1998; Accepted October 16, 1998

Abstract

The factors associated with lobe division were studied in thalli of the lichen *Parmelia conspersa* (Ehrh. ex Ach.)Ach. Lobe division was studied in sequences of adjacent lobes using spatial pattern analysis. In five large thalli, lobe division within the thallus margin was randomly distributed. Correlations between the degree of lobe division, the radial growth of the lobe and lobe morphology were studied in six thalli. Lobe division was positively correlated with either lobe width or area in four thalli. Correlations were observed with radial growth or morphology of the adjacent lobes in two thalli. Dividing and non-dividing lobes were removed from large thalli and glued to pieces of slate with their tips either at the same level or in front of neighbouring lobes. Dividing lobes divided more rapidly when their tips were glued in front of their neighbours. The levels of ribitol, arabitol and mannitol were measured within a 2 mm region of the tip in dividing and non-dividing lobes on four occasions in 1994. Carbohydrate levels were significantly increased in dividing compared with non-dividing lobes. In addition, the mean size of the algal cells was greater in non-dividing compared with dividing lobes especially at the lobe base. However, the percentage of zoosporangia and aplanosporangia did not vary significantly in dividing and non-dividing lobes. These results suggest that: 1) the pattern of lobe division within the thallus margin may be random, 2) lobe division may be determined by lobe size and the location of the lobe tip relative to the neighbouring lobes and 3) there may be an increase in the productivity of lobes associated with lobe division.

Keywords: Lichen, *Parmelia conspersa*, lobe division, ribitol, algal cell division, zoosporangia

*The author to whom correspondence should be sent.

1. Introduction

The margins of foliose and placodioid lichen thalli are composed of individual lobes which grow radially and divide (Hooker, 1980; Hill, 1981, 1984, 1992). In *Parmelia conspersa* (Ehrh. ex. Ach.)Ach., the number of major lobes increases linearly with thallus size (Armstrong, 1991). This suggests that lobe division within the thallus margin is controlled to produce sufficient lobes to maintain the growing perimeter (Hooker, 1980). As a result of lobe division, individual lobes exhibit varying degrees of division of their tips. The degree of division may reflect the time elapsed since the start of the previous lobe division (Armstrong, 1993a, 1995). Hale (1970) observed that the pattern of lobe formation and branching within the margins of foliose lichens was complex. However, there have been few detailed studies on the pattern of lobe division or the factors which influence lobe division.

The present study had four objectives. First, the pattern of lobe division shown by sequences of adjacent lobes was studied using spatial pattern analysis. This analysis determined whether the pattern of lobe division was random or whether clusters of adjacent lobes exhibited similar degrees of lobe division. Second, the extent to which the degree of lobe division was related to the growth and morphology of the lobe or to the characteristics of the adjacent lobes was studied. Third, the relationship between lobe division and the location of the lobe tip relative to the neighbouring lobes was studied. Fourth, lobe division may be associated with changes in the levels of the major carbohydrates at the lobe tip. Hence, the levels of ribitol, arabitol and mannitol, the major carbohydrates found in *P. conspersa* (Armstrong and Smith, 1994), were measured within a 2 mm region of the tip of dividing and non-dividing lobes on four occasions during 1994. In addition, measurements were made of the sizes of algal cells and the proportion of zoosporangia and aplanosporangia in dividing and non-dividing lobes.

2. Materials and Methods

Site

The study was carried out at a site in South Gwynedd, Wales (Nat. Grid Ref. SN 6196) in an area of Ordovician slate described previously (Armstrong, 1974). Fragments of slate with thalli of *P. conspersa in situ* were removed from south and south-east facing rock surfaces. The thalli were placed on horizontal boards in a private garden, located close to the sample site, for a year before the start of the study to allow for acclimatisation.

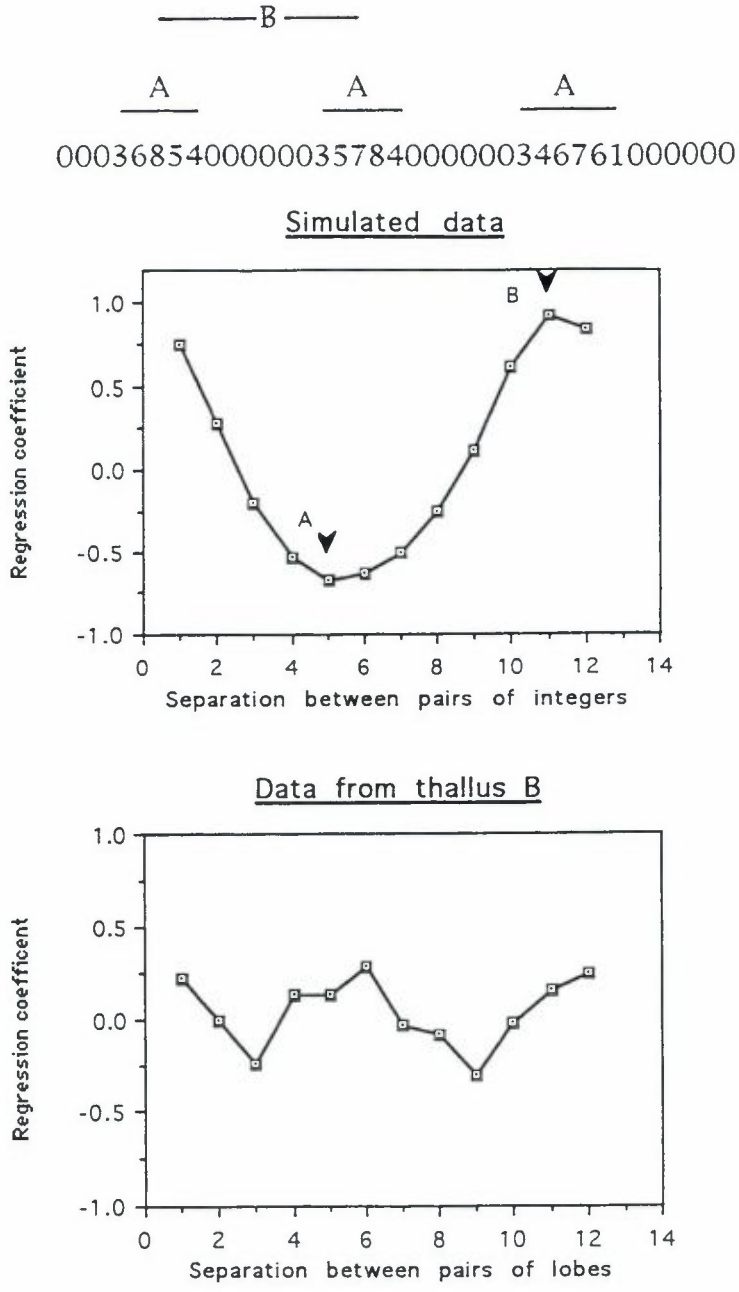

Figure 1. Spatial pattern analysis by regression of the degree of division of a sequence of adjacent lobes within the thallus margin. Model data: analysis of a simulated data set. Data from thallus B: analysis of lobe division from a single thallus (Thallus B) of *Parmelia conspersa*.

Spatial pattern of lobe division

The objective of this study was to determine whether the pattern of lobe division shown by sequences of adjacent lobes was random. Five large (8–10 cm diam.) thalli of *P. conspersa* were chosen for this study. Each thallus had a sequence of at least 20 undamaged major lobes. A major lobe was defined as separated from its neighbour by at least 3 mm of its length on both sides. The division of the tip of each major lobe in the sequence was measured using Vernier callipers. To determine whether lobe division was distributed randomly, the data were analysed by spatial pattern analysis (Yarranton, 1969; Armstrong, 1993b; Armstrong and Wood, 1996). An example of this analysis applied to a simulated set of data is shown in Fig. 1. If the pattern of lobe division was random, regression coefficients calculated from the degree of division of pairs of adjacent lobes and then taken at increasing degrees of separation, i.e., separated by 1, 2, 3, 4, ..., n lobes, would not be significant. However, the simulated data set shows three groups of dividing lobes (A) separated by groups of non-dividing lobes. In this case, positive regression coefficients are observed between adjacent lobes because they show similar degrees of division. However, the regression coefficient falls as the degree of separation between the lobes increases because pairs of lobes are now more likely to show different degrees of division. A significant negative regression coefficient occurs when the degree of separation between lobes corresponds to the mean size of groups of dividing lobes. Finally, a significant positive regression coefficient may occur at the degree of separation between lobes corresponding to the spacing between the groups of lobes (B). The significance of the regression coefficients was tested using 't' tests (Snedecor and Cochran, 1980).

The affect of lobe growth and morphology on lobe division

This study tested whether lobe division was related to the radial growth or morphological characteristics of the lobe itself or to the characteristics of the adjacent lobes. Six thalli of *P. conspersa* were selected at random from the boards and between 10 and 12 major lobes selected at random from each thallus (experimental lobes). Measurements of radial growth and lobe morphology were made on each experimental lobe and on both adjacent lobes. The data from the two adjacent lobes were averaged for each experimental lobe. First, the radial growth of each lobe was measured over two consecutive two month growth periods from 1 April 1991 to 1 August 1991 using previously described methods (Armstrong, 1973). Second, lobe width was measured using a Vernier callipers, 0.5 mm behind the lobe tip. Third, lobe length was measured as the shorter of the two distances from the lobe tip to where the lobe joined its

immediate neighbours or fused with the centre of the thallus. Fourth, lobe area was measured by tracing the outline of the lobe on to 'clingfilm' with a fine nibbed pen (Armstrong, 1992). Fifth, lobe division was measured with Vernier callipers. The degree to which radial growth and aspects of lobe morphology varied between individual thalli was tested by a one-way analysis of variance (ANOVA) (SuperANOVA Software, Abacus Concepts Inc., Berkeley, CA 1989 USA) with comparisons between means made by 't' tests (Snedecor and Cochran, 1980). This analysis suggested significant differences in radial growth and morphology between the individual thalli. Hence, correlations between lobe division, lobe growth and morphology were tested for each thallus using Pearsons's correlation coefficient (Snedecor and Cochran, 1980).

Location of the lobe margin relative to neighbouring lobes

This experiment tested two hypotheses: 1) do non-dividing lobes divide more readily if they protrude from the thallus margin and 2) is the division of dividing lobes restricted by the presence of neighbouring lobes? Non-dividing and dividing lobes were removed from large thalli of *P. conspersa*. These lobes were glued 10 cm apart on large pieces of smooth slate with Bostik No. 1 clear adhesive (Bostik plc, Leicester, UK). Previous studies suggested that gluing treatment had no significant effect on radial growth of this species (Armstrong, 1982). Two lobes were then glued on either side of each experimental lobe to recreate as far as possible the competitive pressures lobes would experience within the thallus margin (Fig. 2). Adjacent lobes were chosen at random from a sample of *P. conspersa* lobes, standardised for width (3–3.5 mm) and degree of division (<1 mm). Adjacent lobes were glued in two orientations relative to the experimental lobes, viz., with their tips aligned at the same level as the experimental lobe or 2 mm behind the experimental lobes. Each of the four treatment combinations was replicated six times. The following data were collected from each experimental lobe at three month intervals from 1, August 1995 until 1, July 1996: 1) radial growth, 2) lobe width, 3) lobe division and 4) number of growth initials using the methods described above. Data analysis was carried out using a two-factor ANOVA.

Levels of carbohydrates in dividing and non-dividing lobes

On four occasions during 1994 (16 March; 3 May; 10 August and 15 October), samples of 20 non-dividing and dividing lobes were removed from several large thalli of *P. conspersa* and divided into four replicate batches each consisting of 5 lobes. Samples were pooled and stored in 70% alcohol in a refrigerator until analysis. Carbohydrates were analysed within a week of collection by gas

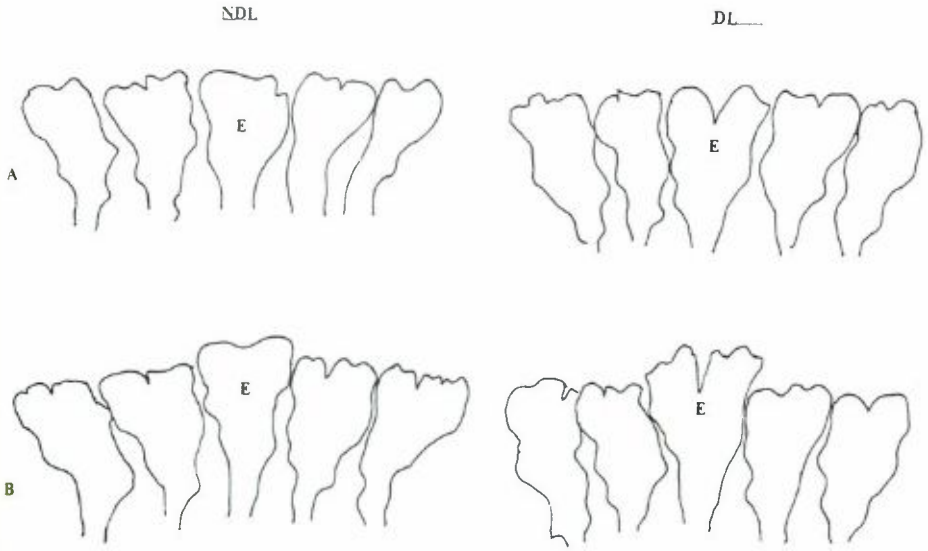

Figure 2. Diagrams illustrating the pattern of gluing of dividing (DL) and non-dividing lobes (NDL) removed from the thallus margin of *Parmelia conspersa*. A) Experimental lobes (E) aligned with adjacent lobes, B) in front of adjacent lobes.

chromatography using the methods described previously (Armstrong and Smith, 1987). Essentially, carbohydrates were extracted from each sample by refluxing in 80% (v/v) ethanol. Subsequently, extracts were silylated and then characterised by capillary gas chromatography. The levels of ribitol, arabitol and mannitol, the major carbohydrates present in *P. conspersa* (Armstrong and Smith, 1994), were determined by reference to known carbohydrate standards added at the initial extraction stage. Carbohydrates were expressed as μg mg biomass^{-1}. Data were analysed using two factor split-plot ANOVA.

Algal cell counts

On 10 August 1998, samples of 10 non-dividing and dividing lobes were removed from several large thalli of *P. conspersa* and frozen. Prior to investigation, the lobes were thawed out and fully hydrated. A 1.5 mm portion cut from the tip and base of each lobe was removed for examination of the algal cells. The greatest diameters of a random sample of at least 50 algal cells were measured at x400 on squashed preparations of lobes using a micrometer scale (Slocum et al., 1980). In addition, the frequency of zoosporangia (four or more segments) and thick-walled aplanosporangia was estimated. Algal sizes and

the percentage of zoosporangia and aplanosporangia in tips and bases of dividing and non-dividing lobes were analysed using a two-factor split-plot ANOVA. Percentages were transformed to an angular scale before analysis (Snedecor and Cochran, 1980). In addition, the frequency distributions of algal cell size at the tips and bases of dividing and non-dividing lobes were compared using chi-square contingency table tests.

3. Results

Spatial pattern analysis of lobe division in a series of sequential lobes is shown for a single thallus (Thallus B) of *P. conspersa* in Fig. 1. None of the regression coefficients were statistically significant at any degree of separation between the lobes. This suggests that the pattern of lobe division in this thallus was essentially random. Similar results were obtained for all six thalli tested (Table 1).

Correlations between the degree of lobe division and the morphology and radial growth of the lobes are shown in Table 2. In 4/6 thalli, a significant positive correlation was observed between lobe division and either lobe width or lobe area. Lobe division was positively correlated with the radial growth of the lobe in the following two month period in only one thallus (Thallus D). In addition, in two thalli (Thalli D, F), lobe division was correlated with the adjacent lobes. In thallus D, lobe division was positively correlated with lobe length, lobe area and the radial growth of the adjacent lobes and in thallus F with division of the adjacent lobes.

Table 1. Spatial pattern analysis of the degree of lobe division in sequences of adjacent lobes within the thallus margin of large thalli of *Parmelia conspersa*.

Thallus	D	N	−Peak	$-\beta_{max}$	't'	+Peak	$+\beta_{max}$	't'
A	10	29	12	−0.20	1.15 ns	11	0.27	1.86 ns
B	11	27	9	−0.30	1.22 ns	12	0.30	1.20 ns
C	8	20	4	−0.19	0.73 ns	1	0.16	0.68 ns
D	8	21	8	−0.25	1.87 ns	3	0.24	0.98 ns
E	10	20	3	−0.44	1.55 ns	6	0.46	1.13 ns

D = thallus diameter (cm); N = number of sequential lobes studied; −Peak and +Peak = the degree of separation between the lobes at which maximum negative and positive regression coefficients were obtained; $-\beta_{max}$ and $+\beta_{max}$ = maximum negative and positive regression coefficients obtained; 't' = 't' test of the regression coefficient; ns = not significant.

Table 2. Correlations (Pearson's 'r') between the degree of division of a lobe (mm) and the morphology and growth (mm in 4 months) of the lobe and of the adjacent (Adj) lobes in six thalli (Th) of *Parmelia conspersa*. (*P<0.05, **P<0.01).

Th	Lobe length	Lobe length (Adj.)	Lobe width	Lobe width (Adj.)	Lobe area	Lobe area (Adj.)	Lobe div. (Adj.)	Radial growth	Radial growth (Adj.)
A	−0.04	−0.17	0.78**	−0.38	0.66*	−0.38	−0.26	0.41	0.06
B	0.64*	−0.48	0.49	0.45	0.81**	−0.14	−0.38	0.46	0.50
C	0.57	−0.16	0.18	−0.06	0.33	−0.10	−0.45	−0.63	0.38
D	0.85**	0.74*	0.82**	−0.15	0.83**	0.73*	0.39	0.71*	−0.18
E	−0.25	0.22	0.28	0.05	0.35	0.09	−0.52	0.54	−0.54
F	−0.05	−0.22	0.65*	0.52	0.39	0.22	0.84**	−0.17	−0.27

Table 3. Influence of the degree of lobe division (mm) and the location of the lobe relative to neighbouring lobes on the radial growth (mm yr^{-1}) of lobes and subsequent lobe division in *Parmelia conspersa*. (***P<0.001, ns = not significant).

Lobes	Non-dividing lobes		Dividing lobes	
Position of lobe	Same level as adjacent lobes	In front of adjacent lobes	Same level as adjacent lobes	In front of adjacent lobes
Radial growth (mm)	0.86	0.70	0.48	0.90
Change in lobe width (mm)	0	0.76	−0.52	1.24
Increase in lobe division (mm)	0.46	0.24	0.20	0.78
Frequency of lobe initials	0.8	1.8	0.6	6.2

ANOVA (two factor): Radial growth, lobes F = 0.14 ns, location F = 0.29 ns, interaction F = 1.46 ns; lobe width, lobes F = 0.42 ns, location F = 16.95***, interaction F = 2.67 ns; lobe division, lobes F = 0.63 ns, location F = 1.04 ns, interaction F = 5.14*; lobe initials, lobes F = 6.12*, location F = 15.13**, interaction F = 7.35*.

The influence of the degree of lobe division and the location of the lobe tip relative to the neighbouring lobes on subsequent division is shown in Table 3. The data suggested that: 1) radial growth of a lobe was not related to its degree of division or location relative to its neighbours, 2) that lobes with their tips in front of their neighbours increased in width regardless of whether they were dividing or non-dividing, 3) non-dividing lobes showed similar degrees of division regardless of location but dividing lobes continued to divide more

Table 4. Levels of ribitol, arabitol and mannitol (μg mg biomass^{-1}) within the tips of non-dividing (NDL) and dividing (DL) of *Parmelia conspersa* on four occasions during 1994.

	Ribitol		Arabitol		Mannitol	
Sample day	NDL	DL	NDL	DL	NDL	DL
16 March	3.14	8.83	8.41	23.46	12.41	29.70
	(0.62)	(1.15)	(1.59)	(2.71)	(1.96)	(2.96)
3 May	2.65	5.90	10.61	21.96	12.13	23.88
	(0.60)	(1.41)	(1.59)	(3.10)	(2.03)	(3.38)
10 August	2.40	4.02	8.43	26.59	10.50	21.84
	(0.59)	(0.14)	(1.25)	(2.31)	(1.89)	(2.94)
15 October	3.06	6.31	9.34	24.09	11.57	25.21
	(1.14)	(0.78)	(0.52)	(2.93)	(3.16)	(2.05)

Analysis of variance (three factor, split-split plot): Main effects type of lobe F = 491.55***, sample day F = 3.22*, carbohydrate F = 332.13***; interactions type of lobe x sample day F = 2.63 ns, carbohydrate x sample day F = 2.85 ns, carbohydrate x lobe tip F = 56.48***.

Table 5. Mean diameter (μm) of algal cells (SE in parentheses) and percentages of zoosporangia and aplanosporangia in non- dividing (NDL) and dividing (DL) lobes of *Parmelia conspersa*.

	NDL tip	NDL base	DL tip	DL base
Mean cell diam. (μm)	8.11 (0.78)	10.43 (10.06)	7.61 (0.74)	9.52 (0.81)
Zoosporangia (%)	7.7 (1.37)	0.6 (0.21)	4.4 (0.76)	0.6 (0.30)
Aplanosporangia (%)	0.83 (0.36)	0.10 (0.08)	1.8 (0.53)	0.35 (0.23)

Analysis of variance (two-factor, split-plot): Algal diameter, NDL v DL F = 4.63*, tip v base F = 61.34***, interaction F = 0.58 ns; % zoosporangia (arcsin transform) NDL v DL F = 1.55 ns, tip v base F = 50.66***, interaction F = 2.56 ns; % aplanosporangia (arcsin transform) NDL v DL F = 3.82 ns, tip v base F = 6.75*, interaction F = 0.35 ns.

rapidly when their tips were located in front of their neighbours and 4) lobes with their tips in front of their neighbours developed more lobe initials and these developed to a greater extent in dividing lobes.

Table 6. Percentage of the total number of algal cells in various size classes in non-dividing (NDL) and dividing (DL) lobes of *Parmelia conspersa*.

Lobe	Location	Size classes (μm) <5	5.1–7	7.1–10	10.1–12	12.1–14	>14
NDL	Tip	0.3	22.5	57.5	16.9	2.6	0
	Base	0	4.5	24.2	43.4	22.5	5.3
DL	Tip	1.4	26.8	48.1	20.7	3.1	0
	Base	0	8.6	36.6	40.3	14.1	0.4

Chi-square (χ^2) contingency tests: DL tip v base $\chi^2 = 103.53^{***}$, NDL tip v base $\chi^2 = 162.90^{***}$, lobe tips DL v NDL $\chi^2 = 8.33$ ns, lobe bases DL v NDL $\chi^2 = 30.44^{***}$.

The levels of carbohydrates within the tips of dividing and non-dividing lobes on four occasions in 1994 are shown in Table 4. The ANOVA suggested: 1) variation in carbohydrate levels between days with highest levels on 16, March and lowest levels on 10, August, 2) a significant interaction between sample day and type of carbohydrate suggesting that the levels of ribitol and mannitol were maximal on 16, March compared with the other sample days while the level of arabitol was maximal on 10, August, 3) dividing lobes contained significantly increased levels of ribitol, arabitol and mannitol and 4) a significant lobe type x carbohydrate interaction suggesting that the arabitol/mannitol ratio was closer to unity (0.95) in dividing lobes compared with non-dividing lobes (0.79).

The mean diameter of algal cells and the percentage of zoosporangia and aplanosporangia in dividing and non-dividing lobes of *P. conspersa* is shown in Table 5. The results suggest that mean algal cell size was greater at the bases than the tips of the lobes and larger in non-dividing compared with dividing lobes. In addition, although the percentage of zoosporangia and aplanosporangia was increased at the lobe tips compared with the lobe bases, there were no significant differences between dividing and non-dividing lobes. The size frequency distribution of algal cell size is shown in Table 6. Lobe tips had a higher proportion of smaller algal cells than the lobe bases. In addition, dividing lobes had a higher proportion of smaller cells at the base of the lobe compared with the non-dividing lobes. This difference was also apparent at the lobe tips but does not reach statistical significance.

4. Discussion

In six large *P. conspersa* thalli, the pattern of lobe division exhibited by sequences of lobes within the thallus margin was essentially random. Hence, lobe division appears to occur more or less independently of the pattern of division of the neighbouring lobes. In addition, in a further six thalli, the degree of division of adjacent lobes was not significantly correlated in five out of six thalli which also supports this conclusion. However, in a single thallus, a positive correlation was observed between lobe division of adjacent lobes.

Lobe division may be associated with two factors. First, lobe division was positively correlated with either lobe width or area. Hill (1992) also found that the distance between successive lobe divisions in *Diploicia canescens* (Dickson) Massal. was related to lobe size. This suggests either that dividing lobes may be larger due to increased lateral growth or that larger lobes are more likely to divide than smaller lobes. Hale (1970) found that growth in width of a lobe ceased when a characteristic width was achieved. In addition, growth experiments suggest that lateral lobe growth is restricted by the presence of neighbouring lobes especially in larger thalli (Armstrong, 1992). These results suggest that lobes may reach a critical size before lobe division can occur (Hale, 1970). Second, although lobe division was not correlated with the growth or morphology of adjacent lobes, the presence of neighbouring lobes could influence lobe division. Dividing lobes divide more rapidly when they protruded beyond their neighbours in the thallus margin. This suggests that the rate of division may be inhibited by neighbouring lobes as a result of a restriction of lateral growth. Hence, lobes which grow slightly beyond their neighbours have a greater chance of reaching a critical size and then of dividing successfully.

The levels of ribitol, arabitol and mannitol were significantly increased in dividing lobes on each sample day. A possible explanation is greater algal cell density in dividing lobes due to increased cell division. However, the present data only partly support this suggestion. The data suggest that algal cells were smaller at the lobe tip compared with the lobe base (Greenhalgh and Anglesea, 1979; Hill, 1993; Honegger, 1996). In addition, mean algal cell size was smaller in dividing compared with non-dividing lobes although this difference was less marked at the lobe tip. The proportion of the smaller cells present (<7 μm), many of which may represent zoospores, was also higher at the tips of dividing lobes. However, there were no significant differences in the proportion of zoosporangia and aplanosporangia in dividing compared with non-dividing lobes. The proportions of sporangia present were highly variable in different lobes and this variability may have masked possible differences between dividing and non-dividing lobes. Alternatively, there may be an increase in the translocation of carbohydrates from the lobe base to the tip in

dividing lobes although this effect has not been demonstrated experimentally (Armstrong and Smith, 1998). Hence, further studies of algal populations in different regions of dividing and non-dividing lobes would be helpful to determine whether the enhanced productivity of dividing lobes is due to changes in algal cell populations.

REFERENCES

Armstrong, R.A. 1973. Seasonal growth and growth rate-colony size relationships in six species of saxicolous lichens. *New Phytologist* **72**: 1023–1030.

Armstrong, R.A. 1974. The descriptive ecology of saxicolous lichens in an area of south Merionethshire, Wales. *Journal of Ecology* **62**: 33–45.

Armstrong, R.A. 1982. Competition between three species of *Parmelia* (Lichens). *New Phytologist* **90**: 67–72.

Armstrong, R.A. 1984. Growth of experimentally reconstructed thalli of the lichen *Parmelia conspersa*. *New Phytologist* **98**: 497–502.

Armstrong, R.A. 1991. Experimental studies of lobe growth in the lichen *Parmelia conspersa* (Ehrh. ex Ach.)Ach. *New Phytologist* **119**: 315–319.

Armstrong, R.A. 1992. A comparison of the growth curves of the foliose lichen *Parmelia conspersa* determined by a cross-sectional study and by direct measurement. *Environmental and Experimental Botany* **32**: 221–227.

Armstrong, R.A. 1993a. Factors determining lobe growth in foliose lichen thalli. *New Phytologist* **124**: 675–679.

Armstrong, R.A. 1993b. The usefulness of spatial pattern analysis in understanding the pathogenesis of neurodegenerative disorders, with particular reference to plaque formation in Alzheimer's disease. *Neurodegeneration* **2**: 73–80.

Armstrong, R.A. 1995. Lobe interactions within the thallus margin and the maintenance of symmetry in the lichen *Parmelia conspersa* (Ehrh. ex Ach.)Ach. *Symbiosis* **18**: 129–142.

Armstrong, R.A. and Smith, S.N. 1987. Development and growth of the lichen *Rhizocarpon geographicum*. *Symbiosis* **3**: 287–300.

Armstrong, R.A. and Smith, S.N. 1994. The levels of ribitol, arabitol and mannitol in individual lobes of the lichen *Parmelia conspersa* (Ehrh. ex Ach.)Ach. *Environmental and Experimental Botany* **34**: 253–260.

Armstrong, R.A. and Smith, S.N. 1998. Does radial growth of the lichen *Parmelia conspersa* depend exclusively on growth processes at the lobe tip? *Environmental and Experimental Botany* **39**: 263–269.

Armstrong, R.A. and Wood, L. 1996 Spatial pattern analysis of ß-amyloid (Aß) deposits in Alzheimer's disease by linear regression. *Alzheimer Disease and Associated Disorders* **10**: 40–45.

Farrar, J.F. 1973. Lichen physiology: progress and pitfalls. In: *Air Pollution and Lichens*. B.W. Ferry, M.S. Baddeley, and D.L. Hawksworth, eds., Athlone Press, University of London, London, pp. 238–282.

Greenhalgh, G.N. and Anglesea, D. 1979. The distribution of algal cells in lichen thalli. *The Lichenologist* **11**: 283–292.

Hale, M.E. 1970. Single-lobe growth rate patterns in the lichen *Parmelia caperata*. *The Bryologist* **73**: 72–81.

Hill, D.J. 1981. The growth of lichens with special reference to the modelling of circular thalli. *The Lichenologist* **13**: 265–287.

Hill, D.J. 1984. Studies on the growth of lichens 1. Lobe formation and the maintenance of circularity in crustose species. *The Lichenologist* **16**: 265–287.

Hill, D.J. 1992. Lobe growth in lichen thalli. *Symbiosis* **12**: 43–48.

Hill, D.J. 1993. The coordination of development of symbionts in mutualistic symbiosis with reference to the cell-cycle of the photobiont in lichens. *Symbiosis* **14**: 325–333.

Honegger, R. 1996. Experimental studies of growth and regenerative capacity in the foliose lichen *Xanthoria parietina*. *New Phytologist* **133**: 573–581.

Hooker, T.N. 1980. Lobe growth and marginal zonation in crustose lichens. *The Lichenologist* **12**: 313–323.

Slocum, R.D., Ahmadjian, V., and Hildreth, K.C. 1980. Zoosporogenesis in *Trebouxia gelatinosa*: ultrastructure potential for zoospore release and implications for the lichen association. *The Lichenologist* **12**: 173–187.

Snedecor, G.W. and Cochran, W.J. 1980. Statistical Methods. 7th edition. Iowa State University Press, Ames, Iowa.

Yarranton, G.A. 1969. Pattern analysis by regression. *Ecology* **50**: 390–395.