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Lobe Interactions within the Thallus Margin and the Maintenance of Symmetry in the Lichen *Parmelia conspersa* (Ehrh. ex Ach.) Ach.

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Abstract

This study determined whether the radial growth of lobes of the foliose lichen *Parmelia conspersa* (Ehrh. ex Ach.) Ach. was influenced by the radial growth and morphology of their closest neighbors and whether such interactions influence thallus symmetry. The radial growth and morphology of a sample of adjacent lobes from six thalli was measured. Positive correlations were observed between radial growth and lobe width in three thalli and with the degree of bifurcation of the lobe in two thalli. Negative correlations between the radial growth of adjacent lobes were observed in four thalli suggesting that faster growing lobes may inhibit the growth of their neighbors. Lobes glued next to individual lobes had no significant effect on the radial growth of wide or narrow lobes. Lobes glued 1–2 mm in front of their neighbors exhibited an initial phase of increased radial growth and then a phase of slower growth. Radial growth decreased when the lobes were glued 2 mm behind their neighbors and these lobes were essentially eliminated by the growth of the adjacent lobes. The data suggest that lobe interactions may increase lobe growth variation within a thallus. However, the decrease in radial growth of lobes which protrude from the margin and the elimination of slower growing lobes may help to maintain thallus symmetry.

Keywords: lichen, *Parmelia conspersa*, radial growth, interactions, lobe division.

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1. Introduction

The margins of foliose lichen thalli comprise individual lobes which grow radially and divide (Aplin and Hill, 1979; Hooker, 1980; Hill, 1984; Armstrong, 1991). The density of marginal lobes is high so that adjacent lobes may interact and compete with each other (Armstrong, 1993). Interactions between adjacent lobes could influence the radial growth and morphology of individual lobes within the thallus margin. Hence, the first objective of this study was to determine whether the radial growth of a sample of lobes was affected by the growth and morphology of their adjacent lobes. This was studied by measuring the degree of correlation between the radial growth of lobes and the growth and morphology of their neighbors in six thalli of *Parmelia conspersa* (Ehrh. ex Ach.) Ach. In addition, lobes were removed from the thallus margin and glued to pieces of slate, with and without lobes glued next to them, to study the physical effects of adjacent lobes on growth. Individual lobes within a thallus may exhibit considerable lobe growth variation (Phillips, 1969; Lawrey and Hale, 1977; Benedict and Nash, 1990; Armstrong and Smith, 1992). However, many foliose lichen thalli observed in the field are relatively symmetrical in shape (Armstrong and Smith, 1992). Hence, the second objective of this study was to determine whether interactions between lobes within the thallus margin influence thallus symmetry. Two aspects of lobe growth could result in thallus asymmetry. First, faster growing lobes, unless restrained by their neighbors, could ultimately grow beyond the thallus margin (Armstrong, 1991). Second, slower growing lobes could result in an indentation within the margin. Hence, lobes were glued either in front of or behind their neighbors to simulate the presence of faster and slower growing lobes within the thallus margin.

2. Materials and Methods

Site and lichens

The study was carried out in South Gwynedd, Wales, U.K. at a site (Nat. Grid Ref. SN 6196) described previously (Armstrong, 1973). All studies were made using approximately circular thalli of *P. conspersa* 3–8 cm in diameter. This species has large, rapidly growing lobes (Armstrong, 1991; 1992). Thalli were removed from various south-facing rock surfaces and were placed on horizontal boards in an unshaded site in the field. Thalli were placed on the boards for at least a year to equilibrate with the environment before they were studied.

Radial growth and morphology of adjacent lobes

The objective of this study was to test whether the radial growth of a sample of marginal lobes was affected by the growth and morphology of their closest neighbors. Six thalli of *P. conspersa* were selected at random and between 10 and 12 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 their closest neighbors. 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 April 1, 1991 to August 1, 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 neighbor or fused with the center of the thallus. This distance could reflect when the lobe was separated from its neighbors. Fourth, lobe area was measured by tracing the outline of the lobe on to 'clingfilm' with a fine nibbed pen (Armstrong, 1992). Fifth, the majority of lobes have divided tips (see Fig. 1), and the extent of division may reflect the time elapsed from the start of lobe division (Armstrong, 1993). Hence, the depth of the bifurcation was measured with Vernier callipers. The degree to which radial growth and aspects of lobe morphology varied between the six thalli was tested by a one-way analysis of variance (ANOVA) with comparisons between means made by t-tests (Snedecor and Cochran, 1980). Since this analysis suggested significant differences in radial growth and morphology between thalli, the data from each thallus were analyzed separately. Hence, correlations between the radial growth and morphology of adjacent lobes were studied within each thallus using Pearson's correlation coefficient (Snedecor and Cochran, 1980). The correlation analysis was used to test two hypotheses: 1) was the radial growth of lobes related to their morphological characteristics, and 2) was the radial growth of lobes related to the radial growth and morphology of adjacent lobes?

Radial growth of lobes removed from the thallus margin

Experiment 1

This experiment compared the radial growth of individual lobes removed from the thallus margin with and without lobes glued next to them. The effect of a lobe on the radial growth of its neighbor may be dependent on lobe width, e.g., a narrow lobe may grow more slowly (Hill, 1992) and therefore, be less able to compete with its neighbors than a wide lobe. To test this hypothesis,

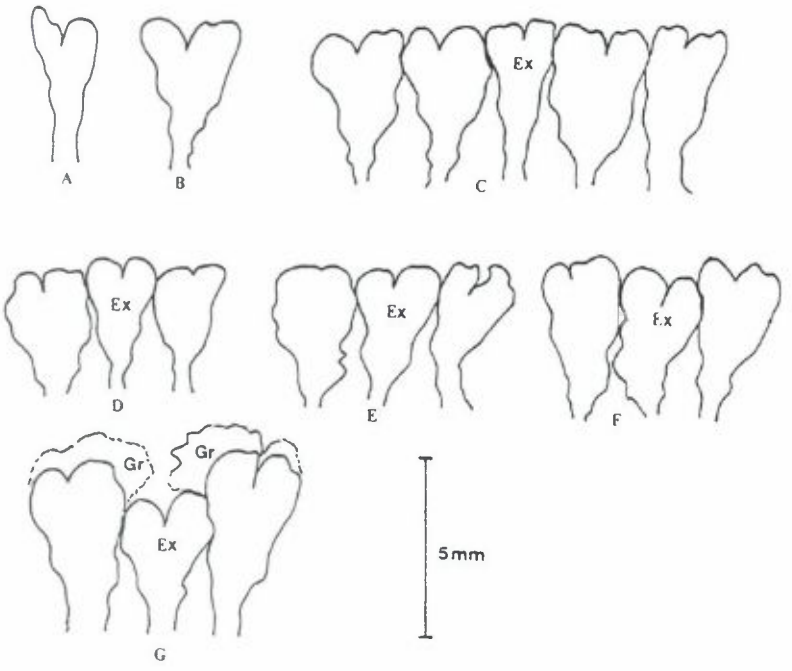

Figure 1. Diagrams illustrating the pattern of gluing of lobes removed from the thallus margin of *P. conspersa* (Ehrh. ex Ach.) Ach. (A, B) individual narrow and wider lobes used in experiment 1; (C) narrow experimental lobe (Ex) with two lobes glued on either side as in experiment 1; (D–G) varying the position of the experimental lobes (Ex) relative to the adjacent lobes in experiment 2: (D) 1–2 mm in front, (E) aligned with, (F) 1 mm behind, and (G) 2 mm behind adjacent lobes. (Gr) indicates the extent of lateral growth of the adjacent lobes over eight months.

two groups of 12 lobes, 1.5–2 mm or 3–3.5 mm in width (Figs. 1A, B), were removed from *P. conspersa* thalli (experimental lobes). These lobes were glued 10 cm apart on large pieces of smooth slate with Bostik No. 1 clear adhesive (Bostik plc, Leicester, U.K.). Previous studies suggested that gluing treatment had no significant effect on the radial growth of lobes of this species (Armstrong, 1982). Half of the lobes of each width were selected at random and two lobes were then glued on either side of each experimental lobe (Fig. 1C). Two lobes were glued to recreate as far as possible the competitive pressures lobes would experience within the thallus margin. Adjacent lobes were chosen at random from a sample of *P. conspersa* lobes standardized for width (3–3.5 mm) and degree of tip bifurcation (<1 mm). The experimental lobes and their neighbors were aligned as closely as possible. Adjacent lobes were glued so that the margins touched but did not overlap. The radial growth

of each experimental lobe was measured at intervals of two months from October 1, 1993 to October 30, 1994 using previously described methods (Armstrong, 1973). The data were analyzed by a two-factor ANOVA to determine: 1) whether the main effects of lobe width and the presence of adjacent lobes affected radial growth of the experimental lobes, and 2) whether the effect of adjacent lobes on radial growth depended on lobe width.

Experiment 2

Lobes which protrude from the thallus margin may grow more slowly than their neighbors (Armstrong, 1993) and slower growing lobes may fall behind their neighbors and be eliminated from the thallus margin (Hooker, 1980). To test these hypotheses lobes were glued in various spatial positions relative to their closest neighbors. Four groups of six lobes (the experimental lobes) were glued to pieces of slate as described in experiment 1. Two lobes were then glued on either side of the experimental lobes as follows (Figs. 1D–G): 1) 1–2 mm behind, 2) aligned with, 3) 1 mm in front, and 4) 2 mm in front of the experimental lobes. Radial growth of each experimental lobe and both adjacent lobes was measured as described previously (Armstrong, 1973) from October 1, 1993 to July 30, 1994. Total radial growth was analyzed by one-way ANOVA and comparisons between means were made using the least significant difference (LSD) at the 5% level of probability. In addition, the two month radial growth measurements were analyzed by a two-factor, split-plot ANOVA with location of the lobe as the major factor and time interval as the minor factor. Comparisons between means were made using the LSD appropriate to the split-plot design (Snedecor and Cochran, 1980).

3. Results

Lobes within the thallus margin

The radial growth and morphology of the experimental lobes and their adjacent lobes for each thallus are shown in Table 1. Variations in lobe growth and morphology were apparent between thalli, e.g., thallus PC5 had the lowest radial growth rate and thallus PC4 had the largest lobes. Variations were also apparent within thalli, e.g., individual lobes varied in radial growth from zero growth to 2.2 mm within a two month period. The degree of lobe variation exhibited by a thallus also varied between thalli with thallus PC5 exhibiting less variation than the other thalli.

Table 1. Mean radial growth (mm) and aspects of the morphology of samples of individual lobes and their adjacent lobes in six thalli of *Parmelia conspersa* (Ehrh. ex Ach.) Ach. (Standard deviations are given in parentheses).

Lobe measurement	PC1	PC2	PC3	PC4	PC5	PC6
A. Radial growth						
First 2 months	0.37	0.23	0.18	0.23	0.1	0.38
	(0.37)	(0.31)	(0.29)	(0.29)	(0.2)	(0.42)
First 2 months	0.31	0.29	0.16	0.31	0.09	0.41
(adjacent lobes)	(0.2)	(0.3)	(0.23)	(0.31)	(0.12)	(0.37)
Second 2 months	1.44	0.97	1.07	1.23	0.43	1.3
	(0.74)	(0.71)	(0.79)	(0.61)	(0.47)	(0.7)
Second 2 months	1.55	1.04	0.98	1.32	0.39	1.4
(adjacent lobes)	(0.48)	(0.58)	(0.68)	(0.38)	(0.31)	(0.39)
Total 4 months	1.82	1.2	1.24	1.36	0.53	1.68
	(0.69)	(0.71)	(0.82)	(0.77)	(0.55)	(0.85)
Total 4 months	1.86	1.34	1.08	1.52	0.45	1.81
(adjacent lobes)	(0.51)	(0.56)	(0.75)	(0.37)	(0.32)	(0.65)
B. Lobe morphology						
Lobe length (mm)	3.42	4.13	2.84	5.3	3.3	3.42
	(0.83)	(1.78)	(0.97)	(1.99)	(0.65)	(0.73)
Lobe length (mm)	3.39	4.19	2.9	5.2	3.55	3.47
(adjacent lobes)	(0.57)	(1.33)	(0.64)	(1.58)	(0.42)	(0.71)
Lobe width (mm)	2.04	1.46	1.56	3.83	1.65	1.44
	(1.1)	(0.51)	(0.77)	(1.32)	(0.77)	(0.58)
Lobe width (mm)	2	1.51	1.59	4.11	1.74	1.49
(adjacent lobes)	(0.56)	(0.4)	(0.76)	(0.94)	(0.77)	(0.37)
Lobe area (mm^2)	7.55	6.32	4.98	22.17	5.47	5.06
	(5.52)	(4.01)	(3.09)	(14.5)	(2.99)	(2.67)
Lobe area (mm^2)	7.34	6.91	5.13	19.91	6.15	5.15
(adjacent lobes)	(3.26)	(3.45)	(3)	(8.23)	(3.05)	(2.4)
Lobe bifurcation (mm)	0.32	0.19	0.14	0.84	0.18	0.15
	(0.38)	(0.29)	(0.15)	(0.45)	(0.12)	(0.23)
Lobe bifurcation (mm)	0.35	0.21	0.14	0.77	0.17	0.15
(adjacent lobes)	(0.38)	(0.23)	(0.11)	(0.37)	(0.06)	(0.14)

Differences between thalli (one-way ANOVA): A) Radial growth, first two months $F = 0.93$ ($P>0.05$); First two months (adjacent lobes) $F = 1.42$ ($P>0.05$); second two months $F = 1.97$ ($P>0.05$); second two months (adjacent lobes) $F = 5.26$ ($P<0.001$); total growth $F = 2.81$ ($P>0.05$); total growth (adjacent lobes) $F = 6.78$ ($P<0.001$); lobe length $F = 4.09$ ($P<0.01$); lobe length (adjacent lobes) $F = 6.35$ ($P<0.001$); lobe width $F = 9.82$ ($P<0.001$); lobe width (adjacent lobes) $F = 22.88$ ($P<0.001$); lobe area $F = 8.7$ ($P<0.001$); lobe area (adjacent lobes) $F = 15.73$ ($P<0.001$); lobe bifurcation $F = 6.78$ ($P<0.001$); lobe bifurcation (adjacent lobes) $F = 7.74$ ($P<0.001$).

Correlations between the radial growth of the lobes and aspects of their morphology are shown in Table 2. No significant correlations were observed between lobe growth and morphology in three thalli. However, in the remaining three thalli, positive correlations were observed in some growth periods between radial growth and lobe size, most consistently with lobe width. In addition, radial growth was positively correlated with the degree of lobe bifurcation in two thalli, i.e., lobes with a greater degree of bifurcation had faster growth rates.

Correlations between the radial growth of the experimental lobes and the growth and morphology of their neighbors are shown in Table 3. Significant correlations were observed between the radial growth of adjacent lobes, either within the same or consecutive growth periods, in four thalli. With one exception (PC5), these correlations were negative, i.e., faster growing lobes were associated with slower growing neighbors. In addition, positive correlations between radial growth and the average length and area of the neighboring lobes were observed in two thalli and a negative correlation with the degree of lobe bifurcation in one thallus.

Lobes removed from the thallus margin

The effect of gluing lobes of *P. conspersa* next to lobes of different width is shown in Table 4. Neither lobe width nor the presence of adjacent lobes significantly affected the radial growth of the experimental lobes. In addition, there was no evidence that the presence of adjacent lobes had a greater effect on narrow than wide lobes. The influence of the position of the lobe relative to its closest neighbors on radial growth is shown in Table 5 and Fig. 2. Lobes glued 1–2 mm in front of their neighbors showed an initial phase of significantly increased radial growth compared with lobes within the margin and then a phase of declining growth (Fig. 2). Total radial growth over 10 months significantly decreased in lobes glued 2 mm behind their neighbors (Table 5). Within eight months of the start of the experiment, lateral growth of the adjacent lobes filled the spaces in front of these lobes (Fig. 1). There was no evidence that the radial growth of lobes adjacent to retarded neighbors significantly increased over the course of the experiment (Table 5).

4. Discussion

The objective of this study was to determine whether the radial growth of a lobe was affected by the growth and morphology of its neighbors and whether lobe interactions may influence the symmetry of the thallus margin. Lobes

Table 2. Correlations (Pearson's 'r') between the radial growth of individual lobes and aspects of their morphology in six thalli of *Parmelia conspersa* (Ehrh. ex Ach.) Ach.

Thallus/growth period	Lobe length	Lobe width	Lobe area	Lobe bifur.
PC1				
First 2 months	0.48	0.3	0.4	0.24
First 2 months (adj.)	0.58	0.74 **	0.77 **	0.37
Second 2 months	–0.06	0.2	0.18	0.27
Second two months (adj.)	0.39	0.36	0.29	0.38
Total growth	0.19	0.37	0.41	0.42
Total growth (adj.)	0.28	0.21	0.14	0.15
PC2				
First 2 months	0.26	–0.28	–0.04	–0.18
First 2 months (adj.)	0.33	–0.33	0.06	–0.19
Second 2 months	–0.21	0.63 **	0.17	0.29
Second 2 months (adj.)	0.07	0.61 *	0.42	0.76 **
Total growth	–0.09	0.47	0.15	0.21
Total growth (adj.)	0.33	–0.33	0.06	–0.19
PC3				
First 2 months	0.18	0.37	0.24	–0.32
First 2 months (adj.)	–0.52	–0.22	–0.27	0.31
Second 2 months	0.07	–0.17	–0.2	–0.33
Second 2 months (adj.)	0.14	0.3	0.33	0.37
Total growth	0.07	0.03	–0.11	–0.32
Total growth (adj.)	0.21	0.17	0.25	0.34
PC4				
First 2 months	0.23	0.31	0.23	0.32
First 2 months (adj.)	0.03	0.35	0.09	0.38
Second 2 months	0.67 *	0.84 **	0.75 **	0.82 ***
Second 2 months (adj.)	–0.29	–0.34	–0.35	–0.37
Total growth	0.37	0.78 *	0.67 *	0.71 *
Total growth (adj.)	–0.33	–0.33	–0.16	–0.33
PC5				
First 2 months	0.08	–0.18	–0.13	0.35
First 2 months (adj.)	0.03	0.06	0.11	0.38
Second 2 months	0.05	0.07	0.05	0.34
Second 2 months (adj.)	0.37	–0.38	–0.15	–0.33
Total growth	0.37	0.06	0.29	–0.39
Total growth (adj.)	0.35	–0.02	0.28	–0.42

Table 2. Continued.

Thallus/growth period	Lobe length	Lobe width	Lobe area	Lobe bifur.
PC6				
First 2 months	0.08	–0.18	–0.13	0.3
First 2 months (adj.)	0.37	–0.38	–0.15	–0.33
Second 2 months	0.03	0.06	0.11	0.38
Second 2 months (adj.)	0.37	0.06	0.29	–0.39
Total growth	0.05	0.07	0.05	0.34
Total growth (adj.)	0.35	–0.02	0.28	–0.42

Adj. = adjacent lobes; bifur. = bifurcation. *P<0.05, **P<0.01, ***P<0.001.

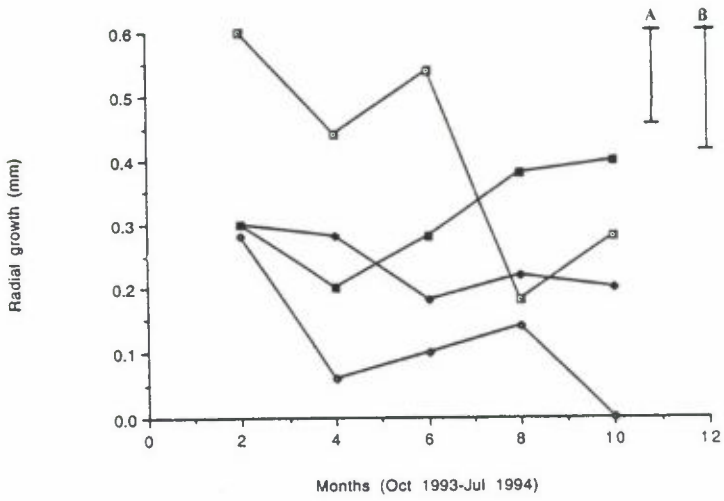

Figure 2. Influence of the position of the lobe relative to the adjacent lobes on the radial growth of individual lobes of *P. conspersa* (Ehrh. ex Ach.) Ach. Location of experimental lobes: (⊡) 1–2 mm in front, (■) aligned with, (♦) 1 mm behind, and (◊) 2 mm behind the tips of adjacent lobes. Error bars indicate the LSD for comparing: A) Treatments within a time interval, B) time intervals within a treatment.

Table 3. Correlations (Pearson's 'r') between the radial growth of a sample of lobes from each of six thalli of *Parmelia conspersa* (Ehrh. ex Ach.) Ach. and the radial growth and morphology of their adjacent lobes.

Thallus/ growth period	Radial growth First 2 months	Second 2 months	Total	Morphology Lobe length	Lobe width	Lobe area	Lobe bifur.
PC1							
First 2 months	–0.61 *	0.16	–0.08	–0.38	0.36	–0.31	–0.39
Second 2 months	0.2	–0.37	–0.28	0.3	0.33	0.3	0.41
Total	–0.11	–0.31	–0.34	0.44	0.37	0.26	0.18
PC2							
First 2 months	–0.2	–0.43	–0.35	0.41	–0.35	0.32	–0.06
Second 2 months	–0.68 *	0.24	–0.12	–0.01	0.17	0.17	0.31
Total	–0.77 **	0.05	–0.36	0.19	–0.07	0.4	0.38
PC3							
First 2 months	–0.48	–0.69 *	–0.72*	–0.45	–0.25	–0.28	0.36
Second 2 months	–0.49	0.12	0.21	0.26	0.37	0.35	0.02
Total	0.34	–0.13	–0.05	–0.09	0.27	0.24	0.21
PC4							
First 2 months	0.13	0.16	0.02	0.04	0.02	0.29	0.35
Second 2 months	0.41	–0.49	–0.29	0.69 *	–0.35	0.68 *	0.34
Total	0.28	–0.39	–0.43	0.39	–0.42	0.37	0.35
PC5							
First 2 months	–0.44	–0.37	–0.46	0.29	–0.22	–0.13	–0.36
Second 2 months	0.33	0.36	0.3	0.21	0.4	0.36	–0.84 **
Total	0.31	0.42	0.25	0.29	0.35	0.43	–0.95 **
PC6							
First 2 months	0.83 **	0.22	0.4	0.85 **	0.43	0.74 *	–0.09
Second 2 months	0.04	–0.66 *	–0.38	0.05	0.07	0.02	–0.13
Total	0.43	–0.42	–0.14	0.44	0.26	0.37	–0.1

Total = total radial growth over 4 months, bifur. = bifurcation. *P<0.05, **P<0.01.

were studied *in situ* within the thallus margin and isolated from the thallus. A disadvantage of the first method is that many factors may influence the radial growth of a lobe within the thallus margin (Armstrong, 1993) and it may be difficult to isolate effects due to adjacent lobes. Removing lobes from

Table 4. The influence of the presence of adjacent lobes on the radial growth (mm in 1 year, standard errors in parentheses) of individual lobes of different width removed from the thallus margin of the lichen *Parmelia conspersa* (Ehrh. ex Ach.) Ach. and glued to pieces of slate.

Lobe width Adjacent lobes	1.5–2 mm Absent	1.5–2 mm Present	3–3.5 mm Absent	3–3.5 mm Present
Radial growth (mm in 1 y)	2.48 (0.49)	2.65 (0.28)	2.15 (0.27)	2.88 (0.1)

ANOVA (two-factor): Lobe width $F = 0.49$ ($P>0.05$), adjacent lobes $F = 2.02$ ($P>0.05$), interaction $F = 0.75$ ($P>0.05$).

Table 5. The influence of the position of the lobe relative to adjacent lobes on the radial growth (mm in 1 year, standard errors in parentheses) of individual lobes of the lichen *Parmelia conspersa* (Ehrh. ex Ach.) Ach.

	Position of experimental lobes 1–2 mm in front of adj. lobes	Aligned with adj. lobes	1mm behind adj. lobes	2mm behind adj. lobes
Radial growth (mm in 1 y)	2.04 (0.31)	1.48 (0.24)	1.56 (0.23)	0.5 (0.31)
Radial growth of adjacent lones (mm)	2.05 (0.3)	1.4 (0.12)	1.75 (0.1)	1.56 (0.13)

ANOVA (one-way): Experimental lobes $F = 5.53$ ($P<0.01$), least significant difference (LSD) = 0.83; adjacent lobes $F = 2.45$ ($P>0.05$).

the margin and gluing them to pieces of slate (Armstrong, 1984) enables the effect of adjacent lobes to be studied directly, the spatial relationships between adjacent lobes to be altered and to standardize experimental lobes but has the disadvantage that conditions within the margin are not exactly reproduced. For example, lobes glued next to one another are not physically joined and therefore, could not exchange carbohydrate through the hyphae (Armstrong, 1991).

In some thalli, there was evidence that wider lobes had faster growth rates. This result would support that of Hill (1992) who established a positive relationship between lobe growth and width in thalli of *Parmelia saxatilis* (L.) Ach. Lack of a positive correlation in some of the thalli studied could be due to the relatively small number of lobes sampled from each thallus. The experiment with glued lobes also failed to demonstrate an effect of lobe width. However, the large standard errors in this experiment may have obscured an affect of lobe width. Large standard errors may have also been responsible for the lack of a demonstrable effect of adjacent lobes on the radial growth of the experimental lobes. However, lobes glued next to each other were not physically joined and this may have reduced the degree of lobe interaction in the experiment. Radial growth was positively correlated with the degree of bifurcation of the lobe in two thalli. This suggests either that radial growth of a lobe may increase immediately after lobe division or that faster growing lobes may divide more often or more rapidly.

Negative correlations were observed between the radial growth of adjacent lobes, either within the same or consecutive growth periods, in four thalli. Negative correlations within the same growth period could result if adjacent lobes exhibited alternating periods of faster and slower growth which were not in phase with each other. However, the radial growth of adjacent lobes in consecutive growth periods should be positively and not negatively correlated if this hypothesis was correct. Alternatively, a fast growing lobe might overgrow the margins of its neighbors thus reducing its size and hence, radial growth (Armstrong, 1993). Negative correlations observed between consecutive growth periods suggest that an interaction between adjacent lobes in a growth period might affect lobe growth in a later period. Positive correlations were observed between lobe growth and the size of the neighboring lobes in some thalli. However, these correlations result from positive correlations between the sizes of adjacent lobes in these thalli. A negative correlation was observed between radial growth and the degree of bifurcation of the adjacent lobes in one thallus. This suggests either that a lobe may grow faster as its neighbor starts to divide or that after division of a lobe there may follow a period in which the radial growth of its neighbor might be restricted.

Hence, lobe interactions could increase the degree of lobe growth variation within the thallus margin. However, the data suggest that there may be mechanisms within the thallus to reduce the consequent thallus asymmetry. The radial growth of a lobe is affected by its position relative to its closest neighbors. First, lobes which protrude 1–2 mm beyond the margin grow more rapidly for an initial period. This may result from a reduction in competition close to the lobe tip allowing a protruding lobe to increase in width. The subsequent decline in radial growth could result from an increasingly

unfavorable microclimate beyond the thallus margin (Armstrong, 1991). Lobes which protrude beyond the margin may dry out more rapidly compared with marginal lobes (Armstrong, 1991), a factor which could reduce their radial growth (Armstrong, 1976). Second, radial growth was reduced when the lobes were glued 2 mm behind their neighbors. This may be due to the lateral growth of the adjacent lobes into the spaces in front of the experimental lobes. Similar results were observed when individual lobes of *P. conspersa* were cut from the thallus margin (Armstrong, 1991). The gaps created were eliminated by the lateral growth of the adjacent lobes within 10 months. Lateral growth of adjacent lobes essentially eliminates the retarded lobes from the thallus margin. Hence, two mechanisms may help to maintain a more uniform thallus margin in *P. conspersa*. First, individual lobes which grow more rapidly than their neighbors and ultimately, protrude from the margin, subsequently slow down until their neighbors catch up. Second, slow growing lobes, which could result in an indentation in the margin, are eliminated by the lateral growth of their neighbors. The data predict that elimination of lobes would commonly occur in *P. conspersa* thalli since first, lobes that fall at least 2 mm behind their neighbors will be eliminated, and second, a lobe could fall 2 mm behind its neighbor in a two month growth period. The elimination of slower growing lobes could result eventually in a thallus margin composed of lobes with similar growth rates and morphologies. Since individual thalli of *P. conspersa* may achieve this state at different times or at different rates in the field, this could explain why *P. conspersa* thalli vary in their degree of lobe variation and in the correlations observed between adjacent lobes.

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