Symbiosis, 15 (1993) 27–49
Balaban, Philadelphia/Rehovot

Radial Growth and Carbohydrate Levels in the Lichen *Parmelia conspersa* on North and South Facing Rock Surfaces

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Received April 17, 1992; Accepted August 10, 1992

Abstract

Parmelia conspersa (Ehrh. ex Ach.)Ach. is a foliose lichen found more frequently on south facing compared with north facing rock surfaces in South Gwynedd, Wales, UK. The radial growth of thalli of *P. conspersa* from a north and a south facing rock surface was measured *in situ* at intervals of two months for 1 yr during 1990/1991. Mean annual radial growth rates were greater on the south compared with the north facing rock surface. In addition, the pattern of radial growth varied during the year with maximum growth recorded in the Feb/Mar. period especially on the south facing rock surface. The levels of ribitol, arabitol and mannitol were measured in individual lobes of *P. conspersa* collected from the same rock surfaces on 4 days (2 Jun.; 7 July and 30 Nov. 1990 and 29 Mar. 1991) during 1990/1991. The total of the three carbohydrates varied between days; the levels of arabitol and ribitol being significantly lower in the 7 July sample on both north and south facing rock surfaces. In addition, the levels of ribitol, arabitol and mannitol were higher on the south facing rock surface especially in the summer samples. The ratio of arabitol plus mannitol to ribitol and the mannitol/arabitol ratio varied more between days sampled than between north and south facing rock surfaces. The level of ribitol in individual thalli was positively correlated with arabitol on the north facing and with mannitol on the south facing slope. These results suggest that differences in the radial growth of *P. conspersa* thalli with aspect are more likely to reflect higher rates of photosynthesis on the south facing rock surface rather than large differences in the way carbohydrates were partitioned on the different surfaces. Lower radial growth rates may place *P. conspersa* at a competitive disadvantage on north facing rock surfaces.

Keywords: *Parmelia conspersa*, radial growth, carbohydrates, rock surface, aspect

1. Introduction

Parmelia conspersa (Ehrh. ex Arch.)Ach. is a foliose lichen found on well lit siliceous rock surfaces of southerly aspect in South Gwynedd, Wales, UK (Armstrong, 1974). It is less common on rock surfaces of more northerly aspect. Lichen populations on north and south facing rock surfaces will be subjected to contrasting microclimates. First, steep south facing rock surfaces have higher levels of photosynthetically active radiation (PAR) for most of the year compared with north facing rock surfaces (Armstrong, 1975). As a result, thalli on south facing surfaces should grow more rapidly than those from north facing surfaces. However, south facing rock surfaces reach higher maximum temperatures especially in Summer. High temperatures may have two effects on lichens. First, the thalli may dry out, resulting in the partial loss of cellular water from both symbiotic partners (Honeggar, 1991). Second, since the thalli may dry out rapidly after wetting, losses of carbohydrate due to resaturation respiration (Smith and Molesworth, 1973) are not likely to be replaced readily by the thallus (Armstrong, 1976). Hence, although south facing rock surfaces may favour greater photosynthesis and growth they are also likely to subject a lichen to greater stress compared with north facing rock surfaces.

Radial growth rate of a lichen on a rock surface will be dependent on the rate of photosynthesis in the alga and the fate of the fixed carbon in the fungus. In *P. conspersa*, which contains *Trebouxia* as the phycobiont, carbohydrate is released from the alga as ribitol and is then converted into arabitol and mannitol in the fungus (Farrar, 1976a, 1973). These soluble carbohydrates may account for up to 10% of the thallus dry weight (Dudley and Lechowicz, 1987; Lewis and Smith, 1967; Mcfarlane and Kershaw, 1985). A major feature of normal metabolism in lichens is the rapid turnover of these carbohydrates (Farrar, 1988) as they provide the substrates for (1) normal respiration, (2) increased respiration after rewetting, and (3) material lost by leakage when a dry lichen is wetted. The levels of fungal carbohydrates are depleted under conditions of stress, e.g. if thalli are kept in the dark (Richardson and Smith, 1965) or are subjected to wetting and drying cycles (Farrar, 1976a). Arabitol may be depleted more rapidly than mannitol, suggesting that the former may act as a short term carbohydrate reserve while the latter may have a more protective function (Farrar, 1973). Mannitol may protect lichens during wetting and drying cycles by (1) reducing the level of osmotica, (2) slowing water loss and (3) protection of macromolecules (Farrar, 1973). As a consequence of microclimatic differences with aspect, there may be differences in carbohydrate production in the alga and in the allocation of carbohydrate in the fungus on north and south facing rock surfaces which could influence radial growth. Hence, this study compares the radial growth of *P. conspersa* thalli on a north and a south facing rock surface with the levels of ribitol, arabitol and mannitol measured in individual lobes.

2. Materials and Methods

Site

The study was carried out in an area of Ordovician slate rock in South Gwynedd, Wales (SN 6196), UK, described by Armstrong (1974).

Climatic records

Climatic records were obtained from the AFRC Institute of Grassland Research, Plas Gogerddan, near Aberystwyth; 8 miles to the south and at the same altitude as the sample site (see Table 1). Corroborating temperature and rainfall measurements were made on a sample of days at the study site and correlated well with the reported data.

Distribution of P. conspersa

Geographical

In the UK, *P. conspersa* occurs on well lit, slightly to markedly nutrient enriched siliceous rock. Three communities have been identified (James, Hawksworth and Rose, 1977): (1) *Parmelion conspersae* which is believed to be the acid rock counterpart to the *Xanthorion parietinae*, (2) *Lecanoretum sordidae* which is richer in crustose species than (1) and (3) *Parmelietum glomelliferae* which is dominated by species of *Parmelia* and *Umbilicaria*.

Local

The distribution of *P. conspersa* at the site was investigated during 1988 on 48 rock surfaces of Ordovician slate. The presence/absence of *P. conspersa* was recorded in 25 randomly located 30×30 cm quadrats placed on each rock surface. The percentage frequency of *P. conspersa* on each rock surface was plotted in relation to slope and aspect on a polar graph using the method described by Pentecost (1979).

Table 1. Climatic data compiled at the AFRC Institute of Grassland Research, Welsh Plant Breeding Station near Aberystwyth, Wales; (A) for the two monthly growth periods and (B) the day of sample collection (TR = Total rainfall in mm, RD = the number of rain days, CC = cloud cover, HS = Hours sunshine, T = Temperature °C, WS = Wind speed m s^{-1}).

A. *Two monthly growth periods*

Period	TR	RD	CC	HS	Tmax	Tmin	WS
June–July 1990	139	29	5.2	6.7	18.9	11.2	3.6
Aug.–Sept.	183	31	5.8	5.3	18.5	11.3	3.1
Oct.–Nov.	274.1	36	6.1	2.2	12.6	6.9	2.9
Dec.–Jan. 1991	232.3	38	6.3	1.8	7.2	1.3	2.5
Feb.–March	128.3	22	6.2	5.3	13.0	5.6	3.2
April–May	140.3	22	6.2	5.3	13.0	5.6	3.1

B. *On day of sample collection*

Day	TR	CC	HS	Tmax	Tmin	WS
2 June 1990	0	7	1.1	15.4	10.3	8.2
7 July 1990	0.9	8	0	17.0	11.9	6.2
30 Nov. 1990	0	8	0	7.6	0.4	0
29 March 1991	0	3	9.3	11.1	0.7	0.51

Growth study

Two steep sided rock surfaces, each with a population of *P. conspersa*, were chosen for this study. One rock surface was approx. north facing (aspect 350°) and the other south facing (aspect 175°). The radial growth of 10 randomly selected thalli from each of the rock surfaces studied was measured at two monthly intervals from 1 June 1990 until 1 July 1991 *in situ*. Between 8 to 10 lobes, selected at random, were measured from each thallus and the data averaged. Radial growth was measured as described by Armstrong (1975) and the data were analysed by a two-factor split-plot analysis of variance with aspect of the rock surface as the major factor and seasonal trend as the minor factor. Individual means were compared by calculating the standard errors appropriate to the split-plot design.

Analysis of carbohydrates

Carbohydrate level may vary significantly between individual lobes of the same thallus and between thalli (Armstrong and Smith, 1992). Hence, both lobes and thalli have to be replicated on each rock surface sampled. Four lobes of similar length and width were cut from each of four large thalli (3 to 8 cm in diameter), chosen at random, from the south and the north facing population. Thalli used for the growth study were excluded. Samples were collected from dry thalli on 4 days during 1990/1991: 2 June; 7 July and 30 Nov. 1990 and 29 March 1991. Samples were stored immediately in 80% ethanol in a refrigerator and were analysed within one week of collection. Carbohydrates were determined by gas chromatography using the method described in detail by Armstrong and Smith (1987). In essence, carbohydrates were extracted from each individual lobe by refluxing in 80% (v/v) ethanol. Subsequently, extracts were silylated and then characterised by capillary gas chromatography. Levels of ribitol, arabitol and mannitol were determined by reference to known carbohydrate standards added at the initial extraction stage. A total of 128 individual lobes of *P. conspersa* were extracted and analysed during this study. Data were expressed as μg of carbohydrate per lobe. Lobes carefully selected for size differed in dry weight by approximately 0.012 mg. An average level of each carbohydrate was calculated for each thallus and these means were analysed by analysis of variance as follows: (1) the total of the three carbohydrates by a two-factor split-plot analysis of variance with rock surface aspect as the major factor and day of collection as the minor factor; (2) on each day, a two-factor analysis of variance with aspect as the major factor and levels of individual carbohydrates as the minor factor; and (3) for each carbohydrate, a two-factor analysis of variance with aspect as the major factor and day of collection as the minor factor. Since there may be differences in the proportions of individual carbohydrates on the different surfaces, the ratio of fungal carbohydrates to ribitol and of mannitol to arabitol were calculated for each lobe and averaged over thalli for each day sampled. In addition, the degree of correlation between the levels of ribitol, arabitol and mannitol in individual thalli was tested separately in the north and south facing samples.

3. Results

The majority of rock surfaces examined were steep sided of southerly aspect (SE, S, SW) or northerly aspect (NE, N, NW) (Fig. 1). *Parmelia conspersa* was present on 21/40 of rock surfaces sampled. The results confirm earlier studies (e.g. Armstrong, 1974) that *P. conspersa* was frequent on south facing rocks and much less common on north facing rocks.

The growth data (Fig. 2) indicate that mean annual radial growth rates were greater on the south compared with the north facing surface (south $\bar{X} = 2.35$ mm yr^{-1}; north $\bar{X} = 0.94$ mm yr^{-1}; 't' = 3.83; P< 0.01). In addition, significant differences in radial growth between the two populations were apparent in the June/Sept. and Feb./March periods. Differences in growth

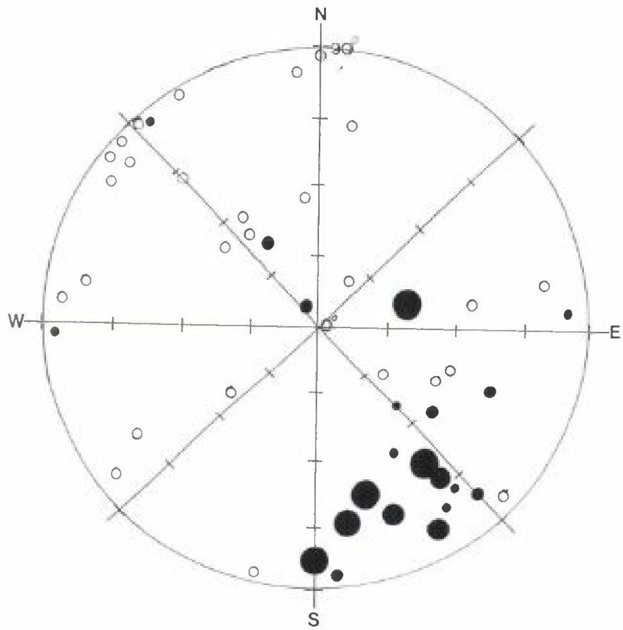

Figure 1. Polar graph showing percent frequency of *Parmelia conspersa* in relation to aspect (distance around circle) and slope (distance along radius). Frequencies are plotted in four bands (•) 0–25%, (●) 26–50%, (●) 51–75% and (●) 76–100%; (o) *P. conspersa* absent.

between the two populations with aspect varied through the year, being least in Oct./Nov. and greater in Feb./March.

The total of the three carbohydrates (Fig. 3) did not vary significantly between south and north facing rock surfaces on the 4 days sampled. However, the total varied significantly between days irrespective of aspect. There was less carbohydrate in the lichen samples on 7 July compared with 2 June and 30 Nov. Results for individual carbohydrates (Fig. 4) indicated that (1) the levels of arabitol and mannitol were greater than the level of ribitol; (2) ribitol levels were greater on the south compared with the north facing rock surface in the 2 June and 7 July samples; (3) the levels of arabitol and mannitol were significantly greater on the south than the north facing rock surface with the exception of the 29 March sample; (4) arabitol and ribitol levels were significantly depleted in the 7 July sample on both rock surfaces; and (5) the level of mannitol appeared to vary less between days than the level of arabitol. The ratios of fungal carbohydrates to ribitol and mannitol to arabitol (Table 2) varied more between days than between north and south facing rock surfaces

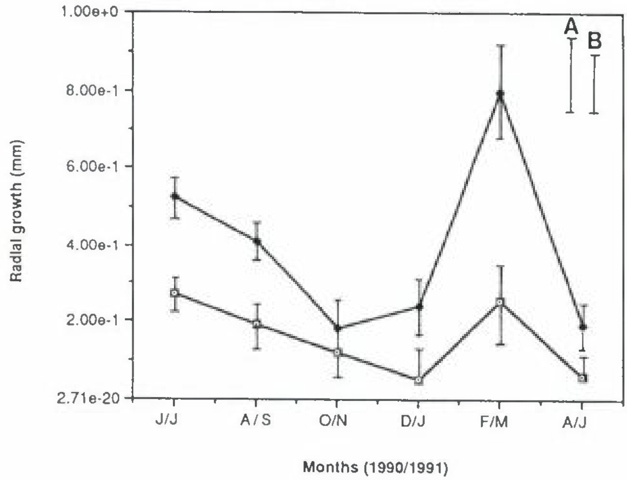

Figure 2. Mean radial growth of of *Parmelia conspersa* thalli on (♦) a south facing and (□) a north facing rock surface during 1990/1991. Analysis of variance: Aspect $F = 14.83$ $P < 0.05$); seasonal trend $F = 15.68$ $P < 0.001$); Interaction $F = 6.15$ $P < 0.05$). (A) Confidence interval for comparing aspect differences. (B) Confidence interval for comparing seasonal differences. Error bars fitted to individual points represent standard errors of the mean.

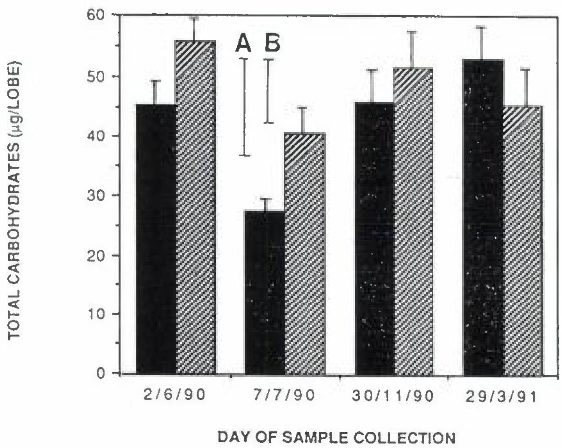

Figure 3. Levels of ribitol + arabitol + mannitol (µg/lobe) in *Parmelia conspersa* thalli from a south facing (hatched histogram) and a north facing (shaded histogram) rock surface. Analysis of variance: Aspect $F = 0.72$ $P > 0.05$); Day of collection $F = 3.92$ $P < 0.05$); Interaction $F = 3.03$ ($P < 0.05$); (A) Confidence interval for comparing aspect differences. (B) Confidence interval for comparing sample days. Error bars fitted to individual histograms as in Fig. 2.

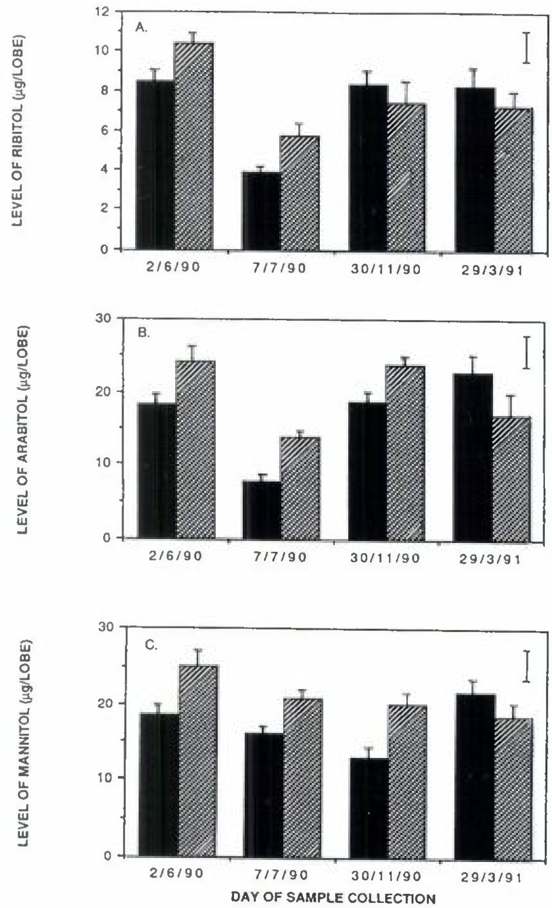

Figure 4. Levels of (A) ribitol, (B) arabitol and (C) mannitol in *Parmelia conspersa* thalli from a south facing (hatched histogram) and a north facing (shaded histogram) rock surface. Analysis of variance: (1) On each day: 2 June, Aspect $F = 7.65$ ($P< 0.05$); Carbohydrates $F = 10.82$ ($P< 0.001$; Interaction $F = 0.91$ ($P> 0.05$); 7 July, Aspect $F = 10.82$ ($P< 0.05$); Carbohydrates $F = 72.60$ ($P< 0.001$); Interaction $F = 2.05$ ($P> 0.05$); 30 Nov, Aspect $F = 1.62$ ($P> 0.05$); Carbohydrates $F = 17.29$ ($P< 0.001$); Interaction $F = 1.69$ ($P> 0.05$); 30 March Aspect $F = 3.49$ ($P> 0.05$); Carbohydrates $F = 25.29$ ($P< 0.001$); Interaction $F = 1.43$ ($P> 0.05$). (2) For each carbohydrate: Arabitol, Aspect $F = 6.52$ ($P< 0.05$); Day of collection $F = 10.46$ ($P< 0.001$); Interaction $F = 1.96$ ($P> 0.05$). Ribitol, Aspect $F = 7.03$ ($P< 0.05$); Day of collection $F = 7.60$ ($P< 0.01$); Interaction $F = 2.58$ ($P> 0.05$). Mannitol, Aspect $F = 0.29$ ($P> 0.05$); Day of collection $F = 0.89$ ($P> 0.05$); Interaction $F = 3.43$ ($P> 0.05$). Error bars fitted to individual histograms as in Fig. 2.

Table 2. The ratio of fungal carbohydrates (arabitol + mannitol) to ribitol (FC/R) and the ratio of mannitol to arabitol in individual lobes of *Parmelia conspersa* from a north (N) and a south (S) facing rock surface.

	FC/R		M/A	
Day	N facing	S facing	N facing	S facing
2 June 90	4.38	4.73	1.01	1.08
7 July 90	6.30	6.10	2.09	1.51
30 Nov. 90	4.77	5.71	0.82	0.84
29 March 91	5.26	4.88	0.95	1.08

Table 3. Correlation (Pearson's r) coefficient matrix between the levels of ribitol, arabitol and mannitol in individual samples of *Parmelia conspersa* thalli collected from a north (N) and a south (S) facing rock surface (R = ribitol, A = arabitol, M = mannitol **P< 0.01; ***P< 0.001).

	S			N		
	R	A	M	R	A	M
R	–	0.47	0.71*	–	0.82***	0.31
A		–	0.45		–	0.30
M			–			–

with the highest ratios recorded on 7 July. The increase in the mannitol/arabitol ratio on 7 July appears to reflect the depletion of arabitol rather than an increase in mannitol. The most notable difference between rock surfaces was the lower mannitol/arabitol ratio on the south facing rock surface on 7 July. Ribitol levels in individual thalli were positively correlated with arabitol on the north surface but positively correlated with mannitol on the south surface (Table 3). Levels of mannitol and arabitol were not significantly correlated in thalli from either surface.

4. Discussion

Radial growth of a lichen thallus will be dependent on the rate of photosynthesis of the alga and the allocation of carbohydrates. In the fungus, carbohydrate will be partitioned between respiration, a soluble carbohydrate pool, structural materials and the polymeric reserve with the soluble pool particularly prone to greater flux (Farrar, 1988). For example, when *Xanthoria aureola* thalli were placed in the dark, mannitol and arabitol levels declined, with mannitol reaching about 30% of it's original level after 5 days (Richardson and Smith, 1965). Preliminary data suggest relatively modest day to day fluctuations in carbohydrate levels (Armstrong and Smith, unpublished data).

However, measurements of carbohydrates made at an instant of time on a limited number of days are likely to reflect specific environmental conditions at the time of sampling and should be used with caution in attempting to explain radial growth measurements made over months.

The total of the three carbohydrates varied between the four days sampled. Levels were depleted on 7 July compared with 2 June and 30 Nov. This depletion results from a fall in arabitol and to a lesser extent in ribitol. The decline in ribitol on 7 July occurred without a significant increase in arabitol or mannitol suggesting a lower rate of photosynthesis. Consistent with this suggestion is the high cloud cover and consequent low PAR on 7 July. In addition, there were several showers of short duration on 7 July (0.9 mm of total rainfall). This, in combination with the high maximum temperature suggests that after wetting, thalli would have dried out rapidly. Wetting could have depleted the level of arabitol in the thalli due to resaturation respiration (Smith and Molesworth, 1973). The level of arabitol may not have been replaced by new photosynthesis because of the rapid drying of the thalli (Armstrong, 1976). Although the absolute levels of arabitol and mannitol were lower on 7 July, the ratio of fungal carbohydrates to ribitol were maximal on both north and south rock surfaces. These results suggest that a higher proportion of carbohydrate was allocated to the soluble fungal pool on 7 July for stress protection. In turn, the lower radial growth rates of *P. conspersa* thalli in summer compared with early spring may be attributable to: (1) the thalli may be dry for long periods, (2) wetting would be followed by fast rates of drying, and (3) a higher proportion of carbohydrate production is allocated to arabitol and mannitol. The higher radial growth rates in Feb./March on the south facing rock surface may be attributable to thalli being moist for longer periods. Although the total rainfall was low in this period, the number of rain days was high and as a result, carbohydrate production would be greater despite lower PAR and temperatures compared with the summer months. In addition, less soluble carbohydrates would be needed for stress protection during this period.

Radial growth rates were higher on the south compared with the north facing rock surface for most of the year. This could be due to the higher levels of ribitol which were recorded on the south facing rock surface on 2 June and 7 July suggesting an increased rate of photosynthesis compared to thalli from north facing rock surfaces. The levels of mannitol and arabitol were also significantly greater on the south facing rock surface on these two days as well as on 30 Nov. Such increases in the absolute levels of arabitol and mannitol may be necessary for increased stress protection (Armstrong, 1975). However, the ratios of fungal carbohydrates to ribitol suggested that there were no large differences in the proportion of carbohydrate production allocated to soluble fungal carbohydrates on both surfaces at least on the days sampled.

Arabitol levels varied more between days than mannitol. These results are consistent with the hypothesis that arabitol is a short term carbohydrate reserve while mannitol has a more protective function (Farrar, 1973). The relationship between the levels of mannitol and arabitol is unclear. Farrar (1973) reported that as arabitol levels fell in the dark, the levels of mannitol rose, suggesting that mannitol could be synthesised from arabitol. Our data do not support this suggestion since the levels of mannitol and arabitol were not significantly negatively correlated on either rock surface, i.e. the levels of arabitol and mannitol appeared to vary independently in individual thalli. However, the correlation data suggest that ribitol in individual thalli may be positively correlated with mannitol on the south face and with arabitol on the north face. The level of arabitol may fluctuate more on south compared with north facing rock surfaces, reflecting the increased levels of stress. The lower mannitol/arabitol ratio on the south compared with the north facing surface on 7 July would be consistent with this suggestion.

The data suggest that although there may be seasonal differences in the allocation of carbohydrates within lichen fungi, these differences are unlikely to explain the radial growth on north and south facing surfaces. The increased annual radial growth rates of *P. conspersa* thalli on the south facing rock surface is likely to be due to increased photosynthesis rather than to differences in the way ribitol is partitioned between growth and soluble carbohydrates. The low frequency of *P. conspersa* on northern rock surfaces at the site could be directly attributable to a reduction in competitive ability as a result of these lower radial growth rates as a consequence of decreased photosynthesis. In a recent study, Armstrong (1991) found that growth in area of *P. conspersa* was reduced when grown experimentally with *P. saxatilis* in northern plots but not in southern plots; a result which would be consistent with this suggestion.

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