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Lobe Connections and Lobe Crowding are Associated with Growth Rate in the Lichen *Xanthoparmelia conspersa*

R.A. ARMSTRONG
Vision Sciences, Aston University, Birmingham B4 7ET, United Kingdom
Tel. +44-121-359-3611, Fax. +44-121-333-4220, Email. R.A.Armstrong@aston.ac.uk

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Abstract

The association between lobe connections and the degree of lobe crowding and radial growth was studied in thalli of the foliose lichen *Xanthoparmelia conspersa*. In 35 thalli, 15% of the lobes were not physically connected to either of their neighbours before the lobes merged into the centre of the thallus. Twenty-five percent of the lobes were connected in pairs and 29% in groups of three. Approximately 5% of the lobes were interconnected in larger groups of six or more. The mean number of lobes per group in a thallus was positively correlated with thallus diameter and with the degree of lobe growth variation but was unrelated to annual radial growth rate (RGR). The degree of crowding of the lobes in a thallus was defined as a 'crowding index', viz., the product of lobe density and mean lobe width. Crowding index increased rapidly with size in smaller thalli but changed less with size in larger thalli. Crowding index was positively correlated with RGR but was unrelated to lobe growth variation. Lobes removed from large thalli and glued in various configurations to simulate different degrees of crowding did not demonstrate an association between lobe crowding and RGR over one year. These results suggest that the pattern of lobe connectivity of a thallus is associated with lobe growth variation in *X. conspersa*. The degree of lobe crowding is associated with the increase in RGR with thallus size in smaller thalli and by restricting lobe width, could also be a factor associated with the more constant growth of larger thalli.

Keywords: *Xanthoparmelia conspersa*, marginal lobes, lobe connections, lobe crowding, radial growth rate, lobe growth variation

1. Introduction

The margin of a foliose lichen thallus is a complex structure consisting of individual lobes which vary in size, shape, branching pattern, and radial growth rate (RGR) (Aplin and Hill, 1979; Hooker, 1980; Hill, 1984; Armstrong, 1991; 1993). It is also a region of intense competition with faster growing lobes overtaking and overgrowing slower growing neighbours (Hooker, 1980). There are two aspects of the growth of foliose lichens which may depend on processes taking place at the margin. First, the RGR of marginal lobes changes with thallus size, increasing in smaller thalli and becoming asymptotic in larger thalli (Proctor 1977, Aplin and Hill, 1979; Hill, 1981; Armstrong, 1996). Second, individual lobes within a thallus show considerable variations in RGR (Phillips, 1969; Lawrey and Hale, 1977; Benedict and Nash, 1990; Armstrong and Smith, 1992).

The influence of various aspects of the biology of marginal lobes on radial growth has been studied previously. The effect of lobe width (Benedict and Nash, 1990; Hill, 1992; Armstrong, 1995), the pattern of lobe division (Armstrong and Smith, 1999), lobe carbohydrates (Armstrong and Smith, 1992), and interactions between neighbouring lobes (Armstrong, 1995) have all been shown to be associated with growth rate. Two factors have been little studied, however, viz., the patterns of connections between lobes (Hill, 1992) and the intensity to which lobes become crowded together and therefore, compete at the thallus margin. Both of these factors could potentially be associated with RGR and the degree of lobe growth variation.

Examination of the marginal lobes show them to exhibit considerable variation in the patterns of branching and therefore, in the extent of the connections with their neighbours, both within and between thalli. Some individual lobes show no physical connections with their neighbours before they merge into the centre of the thallus and lose their individuality while other lobes exhibit a complex branched pattern and occur as groups of interconnected lobes. The first objective of this study was to quantify the degree of lobe connectivity in 35 thalli of *Xanthoparmelia conspersa* and to test the hypotheses that connectivity was related to thallus size, RGR, and the degree of lobe growth variation.

The extent to which lobes are crowded together at the margin also varies between thalli of *X. conspersa* (Armstrong, 1995). In some thalli, individual lobes appear tightly packed together while in other thalli, the lobes appear to be more widely spaced. The second objective of this study was to quantify the degree of lobe crowding in different thalli and to test the hypotheses that changes in the intensity of crowding with thallus size were associated with changes in growth rate of *X. conspersa* (Armstrong, 1996) and with lobe growth variation (Armstrong and Smith, 1992). The effect of lobe crowding was also studied experimentally by removing lobes from the margins of large thalli and growing them in configurations which simulated different intensities of crowding.

2. Materials and Methods

Site and lichens

The study was carried out in south Gwynedd, Wales, UK at a site (National Grid Ref SN 6196) described previously (Armstrong, 1974). All studies were made using approximately circular, healthy thalli of *X. conspersa*. Thalli were originally removed from various south-facing rock surfaces at the site and placed on horizontal boards in an unshaded site in the field, where they remained for at least a year before they were used in a study.

Connections between lobes

The pattern of lobe connections was studied in 35 thalli of *X. conspersa*, 0.4 to 12.5 cm in diameter, drawn from the population on the boards. First, all the 'individual' lobes present at the margin of each thallus were identified and counted. An individual lobe was separated from its neighbours for at least 4 mm of its length measured from the tip, a criterion established in previous studies (Armstrong, 1996). The origin of each 'individual' lobe was then traced back from the margin to the 'centre' of the thallus where the individuality of lobes is lost. If a lobe showed no physical connections with either of its neighbours before merging into the thallus centre, it was regarded as a single unbranched lobe (Fig 1). Some lobes were joined in pairs, or in groups of three, while other marginal lobes were interconnected in larger groups of five or more lobes. Once all the individual lobes in the thallus had been traced, and the number of lobes in each group identified, the connectivity of a thallus was defined as the mean number of lobes per group. To test whether the frequency of the different groups of lobes declined exponentially with increasing number of lobes per group, the frequencies were converted to a logarithmic scale and the degree of linear correlation with number of lobes per group tested using Pearson's correlation coefficient ('r'). The relationship between lobe connectivity and thallus diameter was studied using correlation and regression methods.

Lobe crowding

The degree of lobe crowding was studied in 44 thalli of *X. conspersa* drawn from the population on the boards. Lobe crowding depends both on lobe density and lobe width (Armstrong, 1996), i.e., two similarly sized thalli with equal numbers of lobes would exhibit different degrees of crowding if they differed in mean lobe width. To determine lobe crowding, the density of the lobes at the margin was estimated by dividing the circumference of the thallus by the number of distinct lobes. The width of each distinct lobe was then measured with

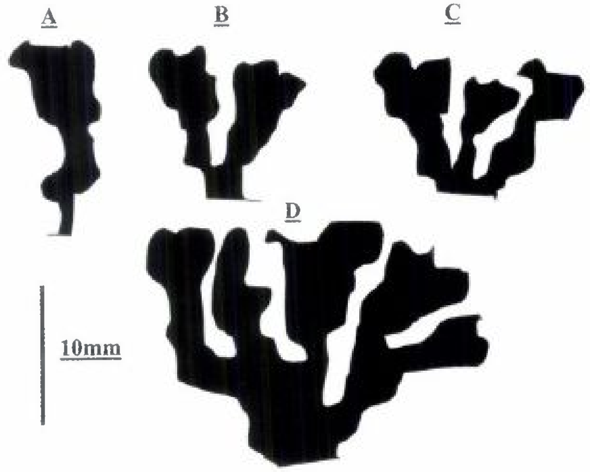

Figure 1. Patterns of lobe connectivity in the lichen *Xanthoparmelia conspersa*: a) single unbranched lobe, b) lobe connected to one neighbour (group of 2), c) lobe connected to both its neighbours (group of 3), d) a group of five interconnected lobes.

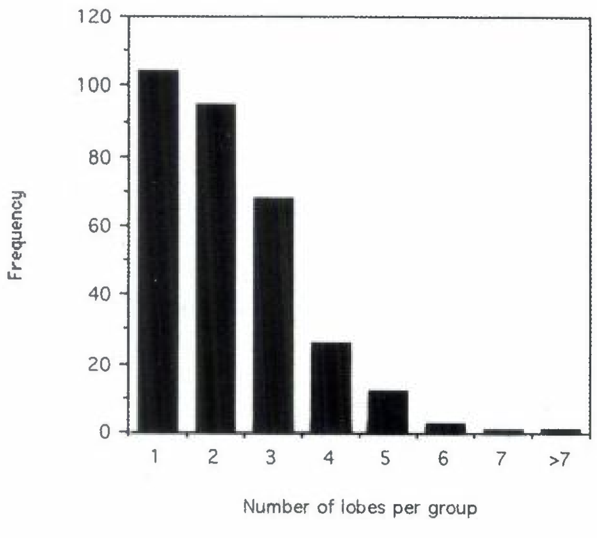

Figure 2. Frequency distribution of the degree of connectivity of the lobes in 35 thalli of the lichen *Xanthoparmelia conspersa*. (Goodness of fit to an exponential model r=0.98, P<0.001).

Vernier callipers 0.5 mm behind the lobe tip (Armstrong, 1996). The 'crowding index' of the thallus was then defined as the product of lobe density and mean lobe width. The relationship between crowding index and thallus diameter was studied using correlation and regression methods.

Relationship between lobe connections, lobe crowding, and RGR

The relationships between lobe connectivity, lobe crowding, and thallus growth was studied in 25 thalli of *X. conspersa* drawn at random from the population on the boards. The degree of connectivity and lobe crowding was determined for each thallus as described above. In addition, the RGR of 8 to 10 randomly chosen lobes was measured for each thallus at three month intervals from Jan 1997 until Jan 1998 using previously described methods (Armstrong, 1973). Radial growth rates were totalled for each lobe and the standard deviation (SD) of these measurements used to describe the degree of lobe growth variation of each thallus (Armstrong and Smith, 1992). In addition, growth increments were averaged and totalled for each thallus to give a measure of annual RGR. Relationships between lobe connectivity, lobe crowding, and thallus growth were studied using correlation and regression methods.

Experimental study of lobe crowding

The objective of this experiment was to compare the growth of lobes cut from the margins of large thalli of *X. conspersa* and grown in various configurations to simulate the effect of different degrees of lobe crowding. Groups of six lobes, 2–3 mm in width, were glued side by side on 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 the RGR of this species (Armstrong 1982). Three configurations were used: 1) the lobes were glued with a space of 0.5 mm between the adjacent lobe tips, 2) the lobes were glued with their margins touching at the tip, and 3) the lobes were glued with their margins overlapping each other by approximately 0.5 mm. Each configuration was replicated five times, the lobes for each configuration being drawn at random from a pool of lobes removed from the thalli. The RGR of each lobe, with the exception of the two flanking lobes, was measured for each configuration at intervals of two months from 1 Aug 1996 to 1 Aug 1997. The data were analysed by a one-way analysis of variance.

3. Results

The frequency distribution of the pattern of connections shown by a sample of 694 lobes from 35 thalli of *X. conspersa* is shown in Fig 2. Fifteen percent of the total lobes sampled were not connected to either of their neighbours before the

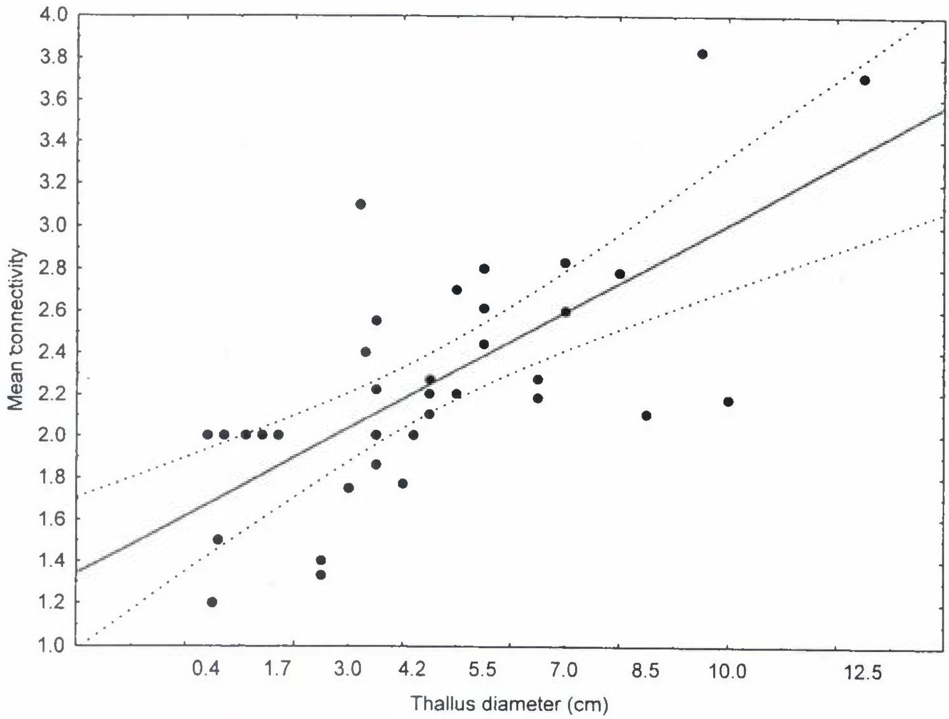

Figure 3. Relationship between mean connectivity of thalli of *Xanthoparmelia conspersa* and thallus diameter (first-order polynomial r=0.70, P<0.001, with 95% confidence bands).

lobe merged into the centre of the thallus. Twenty-five percent of the lobes were connected in groups of two, and 29% in groups of three, while only approximately 5% of lobes were connected in groups of 6 or more. The frequency of particular groupings of lobes declined exponentially with increasing number of lobes per group (r=0.98, P<0.001).

Mean lobe connectivity varied considerably among individual thalli with values in the range 1.2 to 3.83 (mean = 2.25, SD = 0.57). The relationship between mean connectivity and thallus diameter is shown in Fig 3. Lobe connectivity was positively correlated with thallus diameter (r=0.70, P<0.001) suggesting that lobes in smaller thalli were less likely to be physically connected to their neighbours compared with larger thalli. The value of r^2 suggested that 49% of the variance in lobe connectivity between thalli could be attributable to thallus size.

The crowding index of the lobes in different thalli varied in the range 0.19 to 1.0 (mean = 0.67, SD = 0.25). The relationship between crowding index and

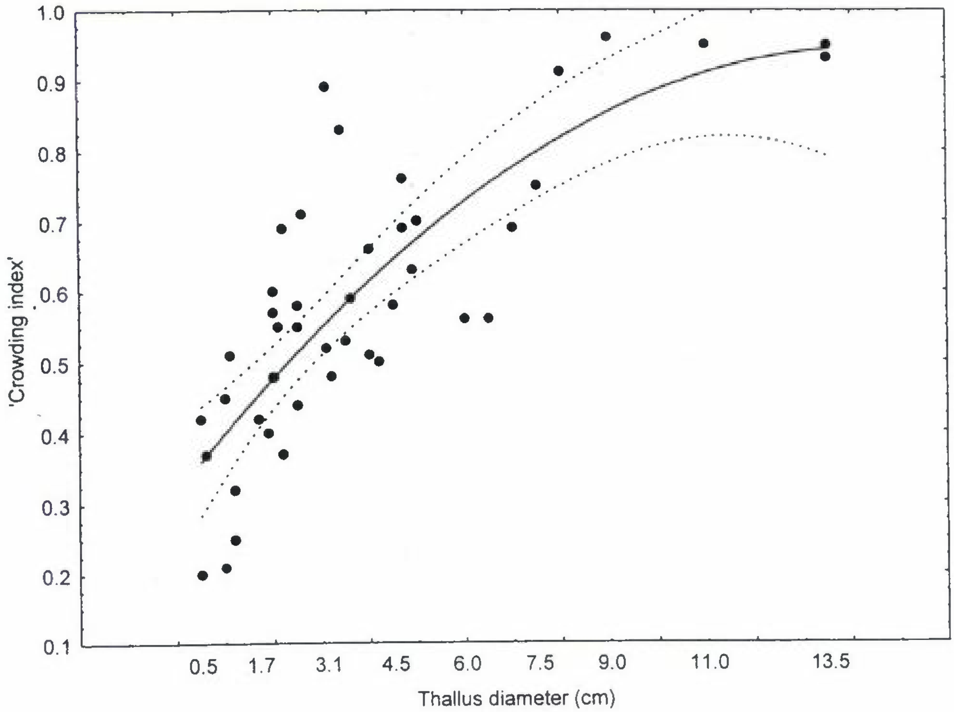

Figure 4. Relationship between the 'crowding index' of thalli of *Xanthoparmelia conspersa* and thallus diameter (second-order polynomial r=0.78, P<0.001, with 95% confidence bands).

thallus diameter is shown in Fig 4. A curvilinear relationship was present significantly different from a linear relationship (second-order polynomial, r=0.78, P<0.001) suggesting that lobe crowding increased rapidly with size in small thalli but to a lesser degree in larger thalli. The 95% confidence bands, however, were wider for larger thalli suggesting that the rate of change in crowding with size was estimated with less confidence as thallus size increased.

Correlations between lobe connectivity, crowding, and aspects of thallus growth are shown in Table 1. Mean connectivity of a thallus was not significantly correlated with RGR (r=0.14, P>0.05) but was positively correlated with the degree of lobe growth variation (r=0.41, P<0.05). Crowding index was positively correlated with RGR (r=0.49, P<0.05), suggesting greater radial growth when the lobes were more crowded together, but was not correlated with the degree of lobe growth variation (r=0.07, P>0.05). There was no significant correlation between the degree of connectivity and lobe crowding (r=0.04, P>0.05).

Table 1. Values of Pearson's correlation coefficient between the mean lobe connectivity (mean number of lobes per group), crowding index, radial growth rate (RGR mm yr^{-1}) and lobe growth variation (SD of lobe growth) in 25 thalli of *Xanthoparmelia conspersa* (*P<0.05).

Mean connectivity	Crowding index	RGR	Lobe growth variation
Mean connectivity	–		
Crowding index	–0.04	–	
RGR	0.14	0.49*	–
Lobe growth variation	0.41*	0.07	–0.12

Table 2. The lack of association between lobe 'crowding' and the mean radial growth rate (RGR mm yr^{-1}) (Standard errors in parentheses) of individual lobes of *Xanthoparmelia conspersa*.

	Degree of crowding of lobes
Lobes separated by 0.5 mm	2.99 (0.28)
Lobes touching	2.96 (0.24)
Lobes overlapping by 0.5 mm	3.29 (0.24)

Analysis of variance (one-way) between groups F = 0.53 (P>0.05).

The association between different degrees of lobe crowding on the growth of individual lobes removed from large thalli of *X. conspersa* is shown in Table 2. Lobe crowding was not significantly associated with RGR of the experimental lobes over one year (F=0.53, P>0.05) although overlapping lobes showed the greatest growth during the experiment.

4. Discussion

There was a considerable degree of variation among thalli in the pattern of lobe connections in *X. conspersa*. Thallus size was one factor associated with this variation, a greater degree of connectivity being observed in larger thalli. There are at least three processes which may influence mean connectivity of a thallus. First, lobe division at the margin, which may be related to lobe size and the location of the lobe tip to that of its immediate neighbours (Armstrong and Smith, 1999), will increase the number of connections between lobes. Second, physical connections between lobes are lost as a result of degenerative processes and fragmentation of the centre of the thallus (Armstrong and Smith, 1997). Third, more slowly growing lobes, and therefore their connections, may be lost as a result of overgrowth and competition (Hooker, 1980). The lack of correlation between crowding and connectivity, however, would argue against this association.

Mean lobe connectivity of a thallus was not correlated with RGR suggesting that changes in the patterns of lobe connections with thallus size were unlikely to be associated with the growth curve of *X. conspersa* (Armstrong, 1996). Mean connectivity was positively correlated, however, with the degree of lobe growth variation; a greater degree of variation being present in thalli with more connections among lobes. Several aspects of lobe behaviour may explain this correlation. First, a group of connected lobes may share carbohydrate among its constituent members (Aplin and Hill, 1979; Childress and Keller, 1980) resulting in reduced intra-group variation but increased inter-group variation. In some thalli, a positive correlation has been observed between the growth of lobes located closest together consistent with this hypothesis (Armstrong and Smith, 1992). Second, individual groups of lobes in a thallus may have different 'parents' (Armstrong, 1984). A previous study demonstrated that an individual thallus may be made up of lobes which originated from several different thalli as a result of the aggregation of thallus fragments in cracks or fissures on the substrate (Armstrong, 1984). Hence, lobes with a single 'genetic' origin may show less variation than lobes which have a different origin. This hypothesis is less likely since lobe growth variation in thalli 'reconstructed' from different individuals was similar to that shown by intact thalli (Armstrong, 1984). Third, lobe competition may be more intense in a thallus comprising connected groups of lobes compared with a thallus made up of single lobes (Armstrong, 1995). A previous study suggested that lobe interactions appeared to increase the degree of lobe growth variation, e.g., a strong competitor could overgrow and reduce the growth of a weaker neighbour (Armstrong, 1995).

The degree of lobe crowding was correlated with thallus size, increasing with size in smaller thalli but changing less in larger thalli. Previous studies have shown that the number of lobes at the margin in *X. conspersa* increases linearly with thallus size but that mean lobe width increases to an asymptotic level (Hale, 1970; Armstrong, 1991). Possible explanations are either that lateral growth of a lobe ceases when a particular width is reached (Hale, 1970) or that further increases in lobe width with thallus size are prevented by increasing thallus crowding. If lobe width changes less with increasing size in larger thalli, both the RGR of larger thalli and the potential of the lobes for further division may be affected (Armstrong, 1995).

The degree of lobe crowding was positively correlated with RGR, i.e., there was greater lobe growth when the lobes were more crowded together or lobes become more crowded when they grow at faster rates. Previous studies have shown that isolated lobes grow more slowly than lobes within the margin possibly as a result of differing microclimates (Armstrong, 1984). These results suggest that changes in lobe crowding with thallus size may be associated with the increase in RGR with size in smaller thalli in *X. conspersa* (Aplin and Hill, 1979; Hill, 1981; Armstrong, 1996). In addition, RGR becomes asymptotic in larger thalli which could also be attributable to the more constant degree of lobe crowding. The RGR of individual lobes over one year, however, was similar in lobes in which different degrees of crowding were experimentally simulated. Therefore, the correlation between crowding and RGR in intact thalli could be due to confounding variables such as lobe width which also increases with thallus size (Armstrong, 1991) and is also associated with RGR (Hill, 1992). Hence, it is possible that as a thallus approaches the linear growth phase, the increasing degree of lobe crowding restricts the lateral growth of the lobes and therefore, lobe width. In larger thalli, there is less change in lobe width with increasing thallus size which could be associated with the onset of the linear growth phase as originally suggested by Hill (1992) in *P. saxatilis*.

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